SCREENING FOR LOW-PHOSPHORUS TOLERANCE AND MYCORRHIZAL RESPONSIVENESS AMONG TOMATO STRAINS

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ABSTRACT

The studies were carried out in order to identify tomato strains (Lycopersicon esculentum) tolerant to low available phosphorus in soil and to determine effect of vesicular-arbuscular mycorrhizal fungi (VAMF) on tomato strains. Low-P tolerance was identified from the comparison of growth under low (P deficient) and high P (P sufficient) conditions. Strains with negligible growth reduction under low P condition were considered low-P tolerant.

Two methods (sand-soil pot and field methods) were used to screen for low-P tolerant tomato strains. Strains 15, 20, 50, 51, 55, 58, 59, 60, 68, 69, 159 and 214 were identified as the potential low-P tolerant strains in sand-soil pot study. Strains 43, 59 and 999 were selected as the low-P tolerant strains in field study.

In order to evaluate how well conclusions drawn from different screening methods correlate with field results, the low-P tolerant screening results from the sand-soil study, a root liquid culture experiment (Coltman, 1987), and a sand-alumina study (Coltman et al., 1985) were all compared to the field results.

The results of screening the low-P tolerant tomato strains in the sand-alumina system (Coltman et al., 1982)

and root liquid culture method (Coltman, 1987) were not significantly correlated with the field study. Screening for low-P tolerance in the sand-alumina and the root liquid culture systems, therefore, can not substitute for field screening studies. However, the sand-alumina system did show potential to screen strains for high P utilization efficiency. Plant growth and P uptake were correlated significantly between the sand-soil and field studies. Sand-soil studies appeared to have good potential to substitute for field studies in screening for low-P tolerant tomato strains.

Inoculation with vesicular-arbuscular mycorrhizal fungi (VAMF) decreased P uptake and plant growth in the sand soil study. In this study, plant were analyzed after only 24 days of growth, and the time was probably too short to allow mycorrhizal symbiosis to increase plant P uptake. This early growth depression was possibly due to VAMF competing for nutrients with the host plants.

In the field study, plants were analyzed after 85 to 100 days of growth. In this period of time mycorrhizal symbiosis became established, and increased P uptake in some strains more than 100%. Strains benefitting most from VAMF inoculation tended to have low p uptake ability. However, not all strains which had low P uptake ability benefitted

from the mycorrhizal symbiosis. Therefore, the presence or absence of mycorrhizae should be considered when making recommendations on low-P tolerant strains.

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CHAPTER 1 LITERATURE REVIEW

INTRODUCTION

Phosphorus (P) is one of the nutrients most frequently limiting crop yields in the highly weathered soils of the tropics such as Oxisols and Ultisols, as well as in soils derived from volcanic ash. The high capacity of these soils to fix P in forms largely unavailable to plants presents serious agronomic and economic constraints. Strategies to improve agricultural production on P-deficient soils emphasize making the most efficient use of available soil P, so that crop production can be sustained with minimum P applications.

A principal component of these strategies is the identification of low-P tolerant crop cultivars or strains. The terminology of plant adaptation to P deficiency stresses is used inconsistently in the literature, so the terminology that will be used in this thesis as follows. "Low-P tolerance" is identified from the comparison of growth under low and high P conditions. Strains with neglible growth reduction under low P conditions are low-P tolerant. "Phosphorus efficiency" is used to describe relative differences in the morphological or physiological mechanisms that contribute to low-P tolerance. Phosphorus efficiency

is commonly measured by P uptake, in total or per unit of root, and the internal P utilization ratio (mg total dry weight per mg P absorbed).

Differential adaptation among tomato strains to low-P availability has been characterized (Coltman et al., 1985). Genes from superior P tolerant strains were readily transferred to intolerant varieties. For example, Coltman (1987) crossed tolerant and intolerant tomato strains and examined the segregating F_2 progeny. Some of the F_2 progeny had higher low P tolerance and P utilization efficiency than either parent.

Plant adaptation to P-deficient soils is believed to involve the development of root systems with morphological and physiological characteristics that improve P absorption. Due to problems with maintenance of soil P concentrations and root recovery in the field, many screening studies for low-P tolerance have been conducted in pots (Caradus et al., 1986, Fox, 1976), sand-alumina media (Coltman et al., 1985), and in solution culture (Coltman et al., 1986, Lindgren et al., 1977, Fawole et al., 1982). However, Caradus et al. (1986) found a poor correlation between low-P tolerance of strains of white clover identified in a solution culture, a greenhouse pot study, and the field. Improved screening techniques for evaluating tolerance to P stress are needed

to accelerate the development of cultivars adapted to low-P soils.

Vesicular-arbuscular mycorrhizal fungi (VAMF) stimulate plant growth by increasing P uptake. The effect is particularly marked on soil of low P fertility. The inoculation of crops with VAMF may provide the solution to producing tomatoes on P-deficient soils. However, the establishment and spread of mycorrhizal infection in plant roots is inhibited by high tissue P (Sanders, 1975). The minimum tissue P concentration required for growth differs between tomato strains, and this may affect the speed and extent of mycorrhizal colonization. The interactions between mycorrhizae and tomato strains may be important for selecting P efficient varieties.

This review is divided into five sections: I) SOIL PHOSPHORUS, II) UPTAKE OF P BY PLANTS, III) POSSIBLE PLANT PHYSIOLOGICAL ADAPTATIONS TO LOW P SOILS, IV) SELECTION FOR P UPTAKE EFFICIENCY and V) MYCORRHIZA AND P UPTAKE.

I. SOIL PHOSPHORUS

Bhat and Nye (1974a) concluded that the P concentration in the soil solution is the major factor controlling the flux of P available to plant roots. Roots deplete the P in

the soil solution surrounding the root surface, thereby creating a gradient between the phosphate concentration near the root surface and the phosphate concentration in the bulk soil (Olsen and Watanabe, 1970). This concentration gradient regulates the rate of phosphate diffusion towards the plant root. Bhat and Nye (1974b) found that the degree of P depletion around onion roots corresponded fairly well with P diffusion calculations. Mass flow also may play a minor role in delivering P to roots (Bole, 1973).

From the viewpoint of plant nutrition, three main soil phosphate fractions are important: 1) phosphate in soil solution, 2) phosphate in the labile pool and 3) phosphate in the non-labile fraction. The first fraction is the phosphate dissolved in the soil solution. The second fraction is the solid phosphate which is held on surfaces so that it is in rapid equilibrium with the soil solution. The third fraction is insoluble phosphate which can be released only very slowly into the labile pool. The amount of phosphate present in the soil solution is very low in comparison with labile phosphate in the highly weathered tropical soils. The quantity of P present in the soil solution, even in soils with a fairly high level of available phosphate, is only in the range of 0.3 to 3 kg P/ha (Mengel and Kirkby, 1982). Rapidly growing crops

absorb P at a rate of about 1 kg P/ha per day. It is clear that the soil solution phosphate must be continuously replenished by desorption of phosphate from the labile pool.

The phosphate available to plants can be assessed by measuring the phosphate concentration in the soil solution and by determining the amount of phosphate released from the labile pool to maintain the soil solution (phosphate buffer capacity) (Olsen and Watanabe, 1970). Fox and Kamprath (1970) showed that wheat yields were highly correlated with P concentration in the soil solution. The concentration of P in soil solutions was a useful indicator of availability of soil P to crops. The concentration of P in the soil solution associated with a particular level of relative yield was also widely applicable across diverse soil types. Fox and Kamprath (1970) also demonstrated that the quantity of P required as fertilizer to adjust the soil P concentration in soil solution can be determined from a P sorption curve. This method provided a basis for determining P fertilizer requirements on soils with varying P adsorption properties. External factors other than solution P concentration also may influence the ability of plants to obtain P from solution. For example, pH (Hendrix, 1967) and the ionic strength of the soil solution (Stanley, 1984b) may strongly influence rate of P absorption by roots.

II. UPTAKE OF P BY PLANTS

Phosphate is taken up by plant cells against a very steep concentration gradient. Generally the phosphate content of root cells and xylem sap is about 100- to 1000-fold higher than that of the soil solution (Russell and Barber, 1960). Phosphate uptake from soil solution into the root is active. Therefore, the factors which affect metabolism, e.g. light intensity temperature and plant status will affect P uptake.

When the concentrations of P in plant tissues approach sufficiency levels, response to P fertilization may be affected by other environmental factors (Lorenz and Vittum, 1980). Samples taken from early growth stages have greater differences in tissue P concentrations between P-deficient and P-sufficient plants (Lorenz and Vittum, 1980). Therefore samples taken early in the growth of plants are more reliable than those taken at a later stage for estimating the plants' nutritional requirements for P.

Optimum external requirements may change with plant growth stage (Fox et al., 1974). For example, corn (Zea mays L.) made maximum early foliar growth with about 0.2 ppm P in soil solution, but grain production was maximized with about 0.05 ppm P. Critical tissue P concentrations in whole

tops declined with age in several pasture grasses (Smith, 1975). The reason for this decline probably lies in the increasing proportion of cells and organs with low P requirements such as stem and senescent leaves compared with those with high P requirements such as meristems and young leaves.

Phosphate deficiency enhances P uptake by roots. Jungk (1974) found that P starvation increased both the maximum P influx and Km (the Michaelis constant) of tomato roots. Stanley (1984a) showed that the number of root hairs also increased when the solution phosphorus concentration decreased.

III. POSSIBLE PLANT PHYSIOLOGICAL ADAPTATIONS TO LOW P SOILS

There are five main physiological characteristics of plants that determine differences among species and varieties in low P adaptability: 1) root morphology and extension, 2) P uptake ability, 3) differential rates of phosphorus utilization and translocation, 4) growth rate, and 5) formation of mycorrhizal associations. The effect of the mycorrhizal symbiosis will be discussed in a later section.

1. Root morphology and entension

The importance of root morphology in P uptake has long been recognized. Barber (1982) showed that total P uptake by the plant was closely correlated with root surface exposed to P. Bray (1954) indicated that only a limited soil volume at the soil-root interface was involved in uptake of immobile ions such as P. Comparing hairless roots and normal roots, Barley and Rovira (1970) found root hairs increased P uptake markedly. Because plant roots remove P from solution much faster than it can be replenished by equilibration with P in the solid phase of the soil, diffusion of P in solution to the root plays a predominant role in the supply of P to roots in soils. Nye (1966) calculated that the P within the root hair zone should be rapidly depleted, because the hairs are densely clustered. Bole (1973) found that increasing the root hair density of wheat did not increase P uptake. However, phosphorus uptake did correspond with the length of root hairs (Brewster et al., 1976). The long root hairs provide a greater surface for P diffusion, and a quick channel for P transport to the root in soil. Phosphorus uptake was also directly proportional to root length, when P uptake was near its maximum rate in the solution (Stanley, 1984b).

Root hairs become very important when P diffusion is low due to low soil P levels. Schenk and Barber (1979) simulated P uptake by corn in high and low P soil. Their model did not account for the effects of root hairs. In the high-P soil, observed and predicted P uptake was not significantly different but in the low-P soil, observed P uptake was double the predicted values. Stanley (1984b) reinterpreted the model. Knowing that corn root hairs are about 0.3 mm in length, he calculated the mean distance over which P would diffuse in four days in the low-P soil to be about 0.63 mm. Hence, root hairs could be important in increasing P depletion of soil near the root. At higher P levels, roots produce fewer and often shorter root hairs increasing the mean diffusion distance between root hairs (0.88 mm), thereby reducing the impact of root hairs on P uptake. Plants actively exploring for P rather than waiting for it to diffuse to their roots, could maintain a sufficient continuous uptake in low-P soil situations, particularly in early growth, thereby increasing their P-use efficiency. Barber (1982) suggests from analysis of his simulation model that increasing root extension and the diameter of the root hair zone may be more effective than developing superior uptake properties in improving plant acquisition of P.

2. P uptake ability

Increasing root surface area increases the potential for P absorption. However, root surface area does not appear to be a major determining factor for efficient P uptake in low P soils. Bole (1973) found rape and flax had very few root hairs compared to wheat, but absorbed more P per unit root length than wheat. The species difference in ion uptake efficiency was not due to root-hair development or root morphology, but rather in P uptake ability. McLachlan (1976) associated the superior P-uptake capabilities of buckwheat with its ability to acidify the rooting medium, presumably via hydrogen-ion extrusion due to excess cation over anion absorption when compared to rye, crimson clover and subterranean clover. Hedley et al. (1982) also showed that the unusually high capacity of rape to extract soil P is due to the acidification of the rhizosphere soil, coincidental with excess cation uptake. Decreasing the rhizosphere pH from 6.5 to 4.1 by proton extrusion, resulted in an estimated ten-fold increase in available P.

Phosphorus uptake ability differs not only between species but also between varieties within a species. Koyama and Snitroongse (1971) found that differences in P accumulation between two rice varieties were not due to

different root growth but to different abilities of absorbing native soil P.

3. Utilization and translocation

McLachlan (1976) found that rye and clover had similar P uptake ability (mg P/ per m root length) but different P utilization efficiency (dry weight g/ mg of P). He concluded that utilization efficiency was more important than P uptake ability in determining growth rate among species. Phosphorus utilization efficiency can vary within species as well. Whiteaker et al. (1976) demonstrated that an efficient bean line produced 74% more dry weight per unit P than an inefficient line. Andrew and Robins (1969) found that forage legume species which are efficient P users tend to have low tissue P requirements to reach maximum growth. Species sensitive to low P concentrations tend to have higher tissue P requirements. This suggests that improving the P utilization efficiency may help the plant adapt to low P soil.

In many species, P stress decreases the size of the tops relatively more than the roots (Williams, 1948). The change in the root:shoot weight ratio appears to result from the ability of deficient root tissues to use absorbed P preferentially for growth of the root system rather than

transferring it to the tops. Nassery (1970) showed that the different growth rate among the species or cultivars may be due to heritable differences in translocation rates of P from roots to tops. Barber (1979) found the root:shoot ratios five corn varieties under similar P stress were significantly different. Fawole et al. (1982) and Coltman et al. (1987) also demonstrated differences within bean and tomato lines in the change in root:shoot ratios during P stress. If harvestable yield is dependent on the P supply, preferential translocation of P to the harvested tissues could be a useful mechanism to incorporate into crops to be grown in P-limited conditions.

4. Growth rate

Slow growth is a important mechanism of native plants for adaptation to soil with low fertility. Barley grass (Hordeum leporinum) was better adapted to infertile soils than barley (Hordeum leporinum L. cv. kombar) due to its slow growth, rather than due to interspecific differences in P absorption or efficiency of P utilization (Chapin, 1982). Asher and Loneragan (1967) also found that the differentially adapted species bromegrass and silvergrass had very similar absorption rates per unit weight of root per day when compared at similar growth rates in flowing

nutrient culture. Differences between these two species in absolute concentrations required for maximum growth are therefore not reflective of different uptake efficiency but rather of differing plant demands due to differing growth rates.

Nye (1966) indicated that a slow relative growth rate allows more time for retranslocation of P from old tissues to the meristems. This permits a more efficient use of P. Clarkson (1967) found that the grass Agrostis setacea grew slower than Agrostis stolonifera at low levels of P. However, A. setacea was able to maintain an exponential increase of dry matter production at low P levels. This suggests that where the P supply is low, the inherently slow growth of a species or strain may be a mechanism for tolerating low soil phosphorus.

IV. SELECTION FOR P UPTAKE EFFICIENCY

Strategies to improve agricultural production on P deficient soils have focused on making the most efficient use of available soil P so that crop production can be sustained with minimum P application. Differential responses among strains to soil P deficiency have been reported in corn (Fox, 1978) white clover (Caradus, 1982), tomato (Coltman et al., 1985) and bean (CIAT, 1981).

Caradus (1979) showed that the root hair length of white clover can be changed by selection. An increase of 50 um in root hair length resulted in a calculated 11% increase in the volume of soil explored by the root hairs. Increasing the absorbing surface of the root may be a possible strategy for improving P uptake. Fawole et al. (1982) crossed P-efficient beans lines and produced progeny which were significantly larger, with more vigorous roots and stable root:shoot ratio, than the parents at both stress and adequate levels of P.

Usually, species or varieties which tolerate low levels of soil P produce maximum yields at lower levels of applied P than do sensitive species or varieties, but they also have lower maximum yields. The goal of breeding programs must be to produce strains adapted to low levels of soil P which also have reasonable yields. Coltman et al. (1987) crossed low-P tolerant and intolerant tomato strains, then produced a backcross generation with the tolerant parent. Some progeny had higher shoot dry weights in low P than any of the parental plants. The progeny had high total P acquisition, high uptake of P per m of root, and efficient internal utilization of P. This indicates that the breeding for adaptation to low P condition has potential to improve productivity in P infertile soils.

V. MYCORRHIZA AND P UPTAKE

Mycorrhizae are soil fungi that form a symbiotic relation with the roots of a host plant. Interactions between host plant and fungus are complex and include reciprocal relationships. The host plant supplies carbohydrates to the mycorrhizal fungi, while benefiting from the fungal relationship through enhanced uptake of immobile, inorganic nutrients.

Mycorrhizae are classified into five groups: ecto-, endo-, ericoid, arbutoic, and orchidacious mycorrhizae. Since the endomycorrhizal association is of greatest importance to agricultural crops, this review will focus on the endomycorrhiza. The group includes the vesicular-arbuscular mycorrhizal fungi (VAMF). Vesicular-arbuscular mycorrhizal fungi are widely distributed geographically and appear to infect most plant species, including the majority of crop species (Mosse et al., 1981). Species belonging to the Cruciferae, Chenopodiaceae and Proteaceae are the only plants of agronomic importance which do not commonly form endomycorrhizal associations. The VAMF infect their host via hyphae which penetrate the epidermis and spread between and into the root's cortical cells. Simultaneously with growth into the root, hyphae grow into the soil. These hyphae have a large surface to volume ratio, compared with

the root-hairs. Therefore they constitute an extra, efficient, well-distributed surface for absorption of immobile ions. Branched hyphal structures called arbuscules and spherical vesicles form within the root. The arbuscules appear to be transfer organs between the fungus and root. Vesicle appear to act as storage organs. The extensive network of mycelium, arbuscules and vesicle do not affect the morphology or function of the root (Harley, 1969).

Mycorrhizal researchers agree that increases in plant growth observed in mycorrhizal plants are due primarily to improved uptake of P. Yost and Fox (1982) found growth rate of cowpea plants in P-deficient soils without mycorrhizae was one-half or less that of mycorrhizal plants. Phosphorus accumulation rates were highly correlated with plant growth rates. Mycorrhizal peppers reached maximum growth at a soil solution P level that was one tenth the concentration required by nonmycorrhizal plants, yet both mycorrhizal and nonmycorrhizal plants had similar maximum yield (Waterer, 1988). This showed that mycorrhizae improve the P uptake efficiency but did not seem to enhance the P utilization efficiency.

Mycorrhizae may increase P absorption in 3 ways: 1) by exploiting a different pool of P than plant roots, 2) by exhibiting more efficient P uptake kinetics than plant

roots, 3) by producing more extensive absorbing structures. Sanders and Tinker (1971) labeled soils low in available P with ^{32}P and then measured specific activities (ratios of labeled to unlabeled P) of the soil solution and of onion roots with and without mycorrhizal colonization. The ^{32}P-^{31}P ratio of phosphorus in plants infected with mycorrhizae was the same as for plant not infected by mycorrhizae. Therefore, mycorrhizae do not appear to extend the phosphorus pool in the soil. Cress et al. (1979) showed that mycorrhizal hyphae had higher affinity to P than plant roots. However, Stanley's (1984a) simulation of phosphorus uptake by hyphae showed that hyphae have similar phosphorus-uptake kinetics to roots. He concluded that the increase in P uptake by hyphae was due to their large absorbing surface, and not any special uptake properties. The longer mycorrhizal hyphae may also take up P more efficiently than the shorter, overlapping root hairs (Baylis, 1975). Because of the overlap in the P uptake zones of root hairs, P concentration at the root surface is lower than at the hyphae face, so the hyphae may be able to absorb P from low-P soil more effectively than the plant root.

Infection by the VAMF does not appear to be influenced by soil pH or texture (Tinker, 1980) but the level of colonization decreases noticeably as the amount of available

P increases (Buwalda et al., 1982). Sanders (1975) demonstrated the establishment and spread of infection in plant roots is inhibited by high tissue P levels rather than by any direct inhibition by high soil P. Ratnayake et al. (1978) noted that plants under P stress experience membrane disfunction, resulting in leakage of metabolites into the rhizosphere. They proposed that mycorrhizal fungi may respond to this chemical stimuli in a manner which ultimately leads to increased colonization in P stressed plants.

Regardless of the mechanisms involved, the symbiosis appears to be largely self regulatory. Colonization progresses when the plant will benefit from the resulting increased P uptake. When the supply of P from the soil is adequate, colonization is suppressed, thereby avoiding the costs of the symbiosis when the added nutrients would be superfluous. Tinker et al. (1982) indicated that 10 to 12% of the carbon that would normally go into the shoot of the host goes to the root in plants infected with mycorrhizae. The soil phosphorus level above which mycorrhizae do not benefit plant growth must be one where roots plus root hairs can absorb sufficient phosphorus to maximize plant growth. Daft and Nicholson (1969) illustrate the effect of cumulative P application on growth and mycorrhizal

colonization of corn and tomato. When P applications were low, root colonization was high and mycorrhizae had a beneficial effect on plant growth. As fertilizer P was increased, the growth benefits due to inoculation were lost and colonization declined.

The interactions between the mycorrhizal fungus and plants are complicated. Azcon and Ocampo (1981) found the speed and extent of VAMF colonization differed between wheat strains. Mycorrhizal colonization correlated with the root weight and root carbon exudate, but not with the tissue P concentration. However, the factors affecting the affinity between mycorrhiza and host were not yet completely understood. Efficient mycorrhiza-host combinations may achieve higher productivity than efficient P strains alone. Therefore, different interactions between mycorrhiza and host strains may be important during development of low-P adapted and P-efficient crop strains.

CHAPTER 2 THE POT STUDIES

INTRODUCTION

Low input agricultural strategies are currently being formulated for less developed countries where the low availability of phosphorus (P) in the soil is a major constraint in the production of food crops. The identification of genetic variability among and within crop species for low P tolerance is required before breeding for improved productivity on low P soil. Strains of tomato (Coltman et al., 1985), corn (Fox, 1978), beans (Salinas, 1978), bean (CIAT, 1981) and white clover (Caradus, 1982) have shown genotypic variation in low P tolerance. Coltman et al. (1985) showed that when a low-P tolerant tomato strain was crossed with an intolerant strain, some progeny grew better under low P conditions than either parent. Therefore, the improvement of popular tomato varieties by crossing them with low-P tolerant strains shows considerable promise.

Fox et al. (1979) determined that the phosphate concentration in soil solution controlled its availability to the plant. However, maintaining P concentrations in the field is very difficult (Barrow et al., 1977). Screening varieties in pots, which require small amounts of soil and

can be given uniform applications of P, is a common and convenient method employed in P efficiency studies. In order to screen a large germplasm collection with minimal cost and space, it is necessary to do the screening at an early stage of plant growth. Tremblay and Baurs (1952) also showed that plants were more sensitive to available phosphate and phosphate deficiency during early growth than during later stages of growth. Thus, examining young plants may be necessary to identify P tolerant strains.

Reducing growth and preventing fluctuation of tissue P concentrations are two important mechanisms by which plants adapt to P deficient soil (Rorison, 1968). However, reducing growth decreases yields which defeats the goal of increasing productivity on P deficient soil. Some plants adapt to P deficient soil by increasing P utilization efficiency and do not reduce growth (Andrew and Robins, 1969). Therefore, P tolerant strains that take up and utilize P efficiently without decreasing growth could prove very important in increasing yields on P deficient soils.

The main benefit of infection with vesicular-arbuscular mycorrhizal fungi (VAMF) is to increase P uptake, particularly in plants growing in low-P soils. Mycorrhizal colonization rate and extent of colonization differ between wheat strains (Azcon and Ocampo, 1981) and may also differ

between tomato strains. Selecting for a P-efficient symbiosis between mycorrhizae and host plants may be an important factor in determining low-P-tolerant tomato strains.

The objective of these studies was to determine the extent of genotypical variability among tomato strains for low-P tolerance, and of strain-specific mycorrhizal effects on P uptake ability. The mechanisms involved in differential dry weight accumulation in terms of P uptake and internal P utilization efficiency (dry weight produced per mg of P uptake) also were examined. Responsiveness of the various strains to mycorrhizal inoculation was measured by the ratio of mycorrhizal P uptake versus nonmycorrhizal P uptake (M/N P uptake ratio).

EXPERIMENT 1 -SCREENING P TOLERANT TOMATO STRAINS IN POT

MATERIALS AND METHODS

Twenty tomato strains (Lyopersicon esculentum) Fig. 2.1 were used in this study. These strains were collected and maintained by Dr. R. R. Coltman, Department of Horticulture, University of Hawaii. Plant introduction and accession numbers as well as the origin of these strains are presented in Appendix Table A. The accession numbers were used to identify the tomato strains in this experiment

Two P concentrations in soil were used to screen the low-P tolerant strains. The medium for the experiment was a 1:1 (by volume) mixture of Waialua clay soil (Vertic Haplustoll) and basaltic sand. Extractable P concentrations of the medium were 0.075 mg/liter (high P level) and 0.024 mg/liter (low P level) before adding phosphate. Treble superphosphate at 1.14 g/kg and KNO_3 at 0.7 g/kg of soil/sand mixture was added to both the high P and low P media. The P was equilibrated by imposing 3 dry/wet cycles in a 15 day period. After equilibration, soil solution P concentrations were 0.1 (high P level) and 0.03 (low P level) mg P/liter as determined by desorption in 0.01 M $CaCl_2$ (Fox and Kamprath, 1970). The soil was fumigated with methyl-bromide/chloropicrin two weeks before planting.

The seeds of the tomato strains were sterilized by dipping them in 1% sodium hypochlorite for 5 minutes and then were germinated in petri dishes. The seeds were transplanted into 900 ml of pots after 5 days at which time the radicles were about 0.5 cm long. Mycorrhizal treatments were inoculated with 150 spores per pot of the VAMF Glomus aggregatum at transplanting. One hundred ml of KNO_3 (500 mg /liter) was added to each pot on the 18th day after transplanting.

Pots were randomly arranged on a greenhouse bench at the Magoon Facility, Department of Horticulture, University of Hawaii. The average daily maximum and minimum temperatures during the experimental period were 41.6^{o}C and 23^{o}C, respectively.

Plants were harvested on April 14, 1987 after 24 days of growth and dried in a oven at 60^{o}C. Plant shoot dry weights recorded and tissue P concentration was determined colorimetrically (Murphy and Riley, 1962) after dry ashing at 550^{o}C.

Data were analyzed as a factorial experiment with tomato strain (twenty strains), P level (0.1 and 0.03 mg P/ liter soil solution) and mycorrhizae (noninoculated and inoculated) as factors with four replications.

RESULTS AND DISCUSSION

P effects

Growth of strains 54, 56, 57, 61, 65 and 66 was significantly depressed at low P and these strains were considered low-P intolerant (Fig. 2.2). Some of the low-P tolerant strains may have had sufficient P for optimal growth at low P and accumulated high P levels in tissues at high P. For example, strain 50 had markedly different total P uptake (Fig. 2.1) between high and low P levels, but dry weights were similar at both P levels (Fig. 2.2). Strains 58, 59 and 60 had significantly lower dry weight at high P than at low P. These three strains seemed to suffer P toxicity at the high P level (Fig. 2.2).

Even though plant growth at the high P level cannot be used confidently as an "optimum P" reference level from which to measure the growth depression at the low P level, a number of "probably-P-tolerant strains" can be identified in this study. Strains 58, 59 and 60 grew well at low P and suffered from P toxicity at the high P level (Fig. 2.2). Strains 50, 51, 55, 68 and 69 had similar growth at high P and low P level. Because of the apparent low external P requirement for optimal growth of these strains, they were identified as " probably-low-P tolerant strains".

Nishimoto et al. (1977) determined that tomato plants

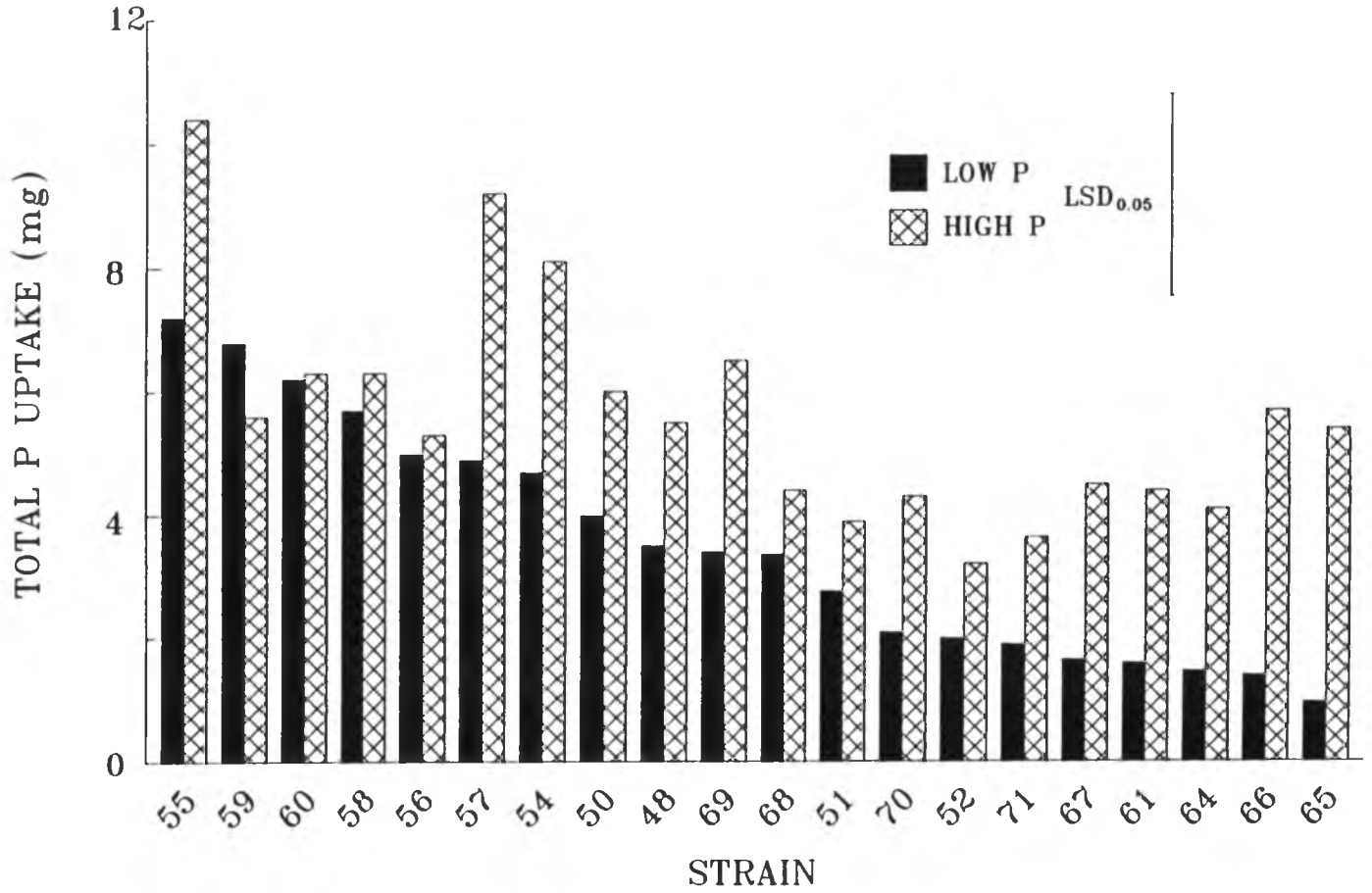

Fig. 2.1. The total P uptake of 20 tomato strains at low (0.03 mg/liter) and high (0.1 mg/liter) soil solution P concentrations in Experiment 1.

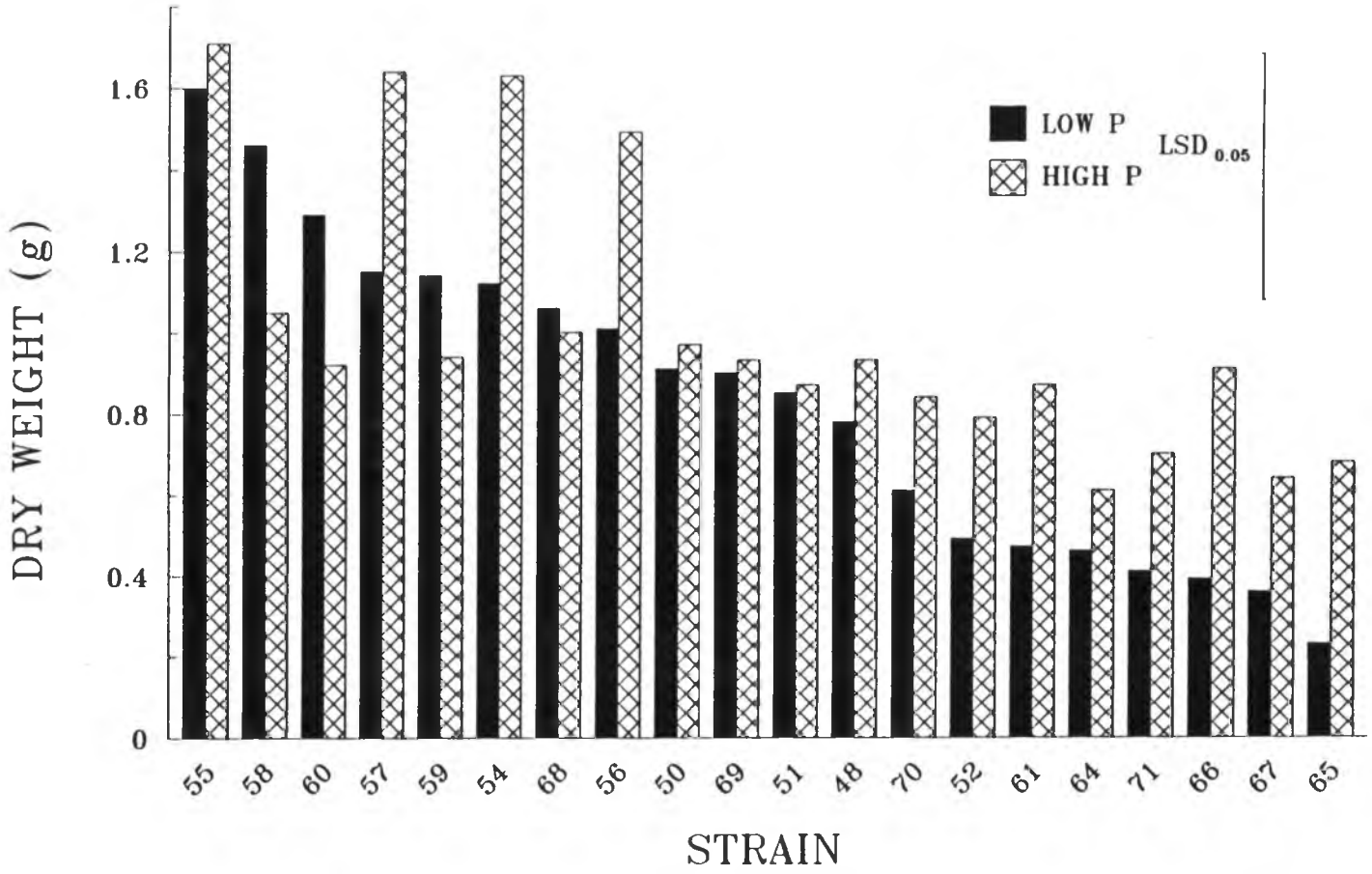

Fig. 2.2. The dry weight accumulation of 20 tomato strains at low (0.03 mg/liter) and high (0.1 mg/ liter) soil solution P concentrations in Experiment 1.

produced 90% maximum fruit yields at 0.1 mg P/liter soil solution, and attained only 70% of maximum growth at 0.03 mg/liter. However, the present experiment indicates that 0.1 mg/liter soil solution P does not produce maximum vegetative yields in all strains. Indeed, this high level of P depressed growth in several strains. This difference in P requirement may have been caused by slow plant growth or a varying P requirements at different growth stages. High temperatures in the greenhouse and the compactness of the soil/sand medium might have inhibited normal plant growth. The plants' internal P requirement may have been satisfied by the low external P concentration due to slow growth. Twenty-four days also may have been insufficient for strains to express their differences. Finally, the growth difference between 0.03 and 0.1 mg/liter soil solution P was 20% in Nishimoto's experiment, but because of variability, in the present experiment growth difference less than 30% cannot be detected and the low-P tolerant strains could not be separated from intolerant ones.

Theoretically, in screening for low-P tolerance, the high P treatment should support near optimum growth, but not cause efficient P strains to suffer toxic effects. The low P treatment should decrease plant growth of the inefficient P strains, enabling separation of plants into tolerant and

intolerant strains. In this experiment, the high P treatment (0.1 mg/liter) and the low P treatment (0.03 mg/liter) seemed too high to meet these goals. The determination of suitable P concentrations for screening strains consequently was examined in the next experiment.

Mycorrhizael effects

Mycorrhizae depressed P uptake (Fig. 2.3) and dry weight (Fig. 2.4) of most of the strains in this experiment. Depressed growth caused by mycorrhizal infection has also been reported in tomato plants infected with G. macrocarpus (McGraw and Schenck, 1980), in pearl millet infected by G. fasciculatum (E3) (Krishna and Dart, 1984), in alfalfa infected with G. monosporum (O'Bannon et al., 1980) and in Hdedysarum coronarium infected with G. caledonium. BethenFalvay et al. (1983) showed that mycorrhizae not only competed for available phosphate with the host, but also intercepted carbohydrates in the inoculated plants. In the present study, mycorrhizae may have competed with the host plant for limited available P, and carbohydrate, and thereby caused the severe growth depression of most of the strains.

Only three strains (65, 66 and 67) benefited from mycorrhizal inoculation (Fig. 2.3). These strains had very slow growth at low P level. Eventhough these strains

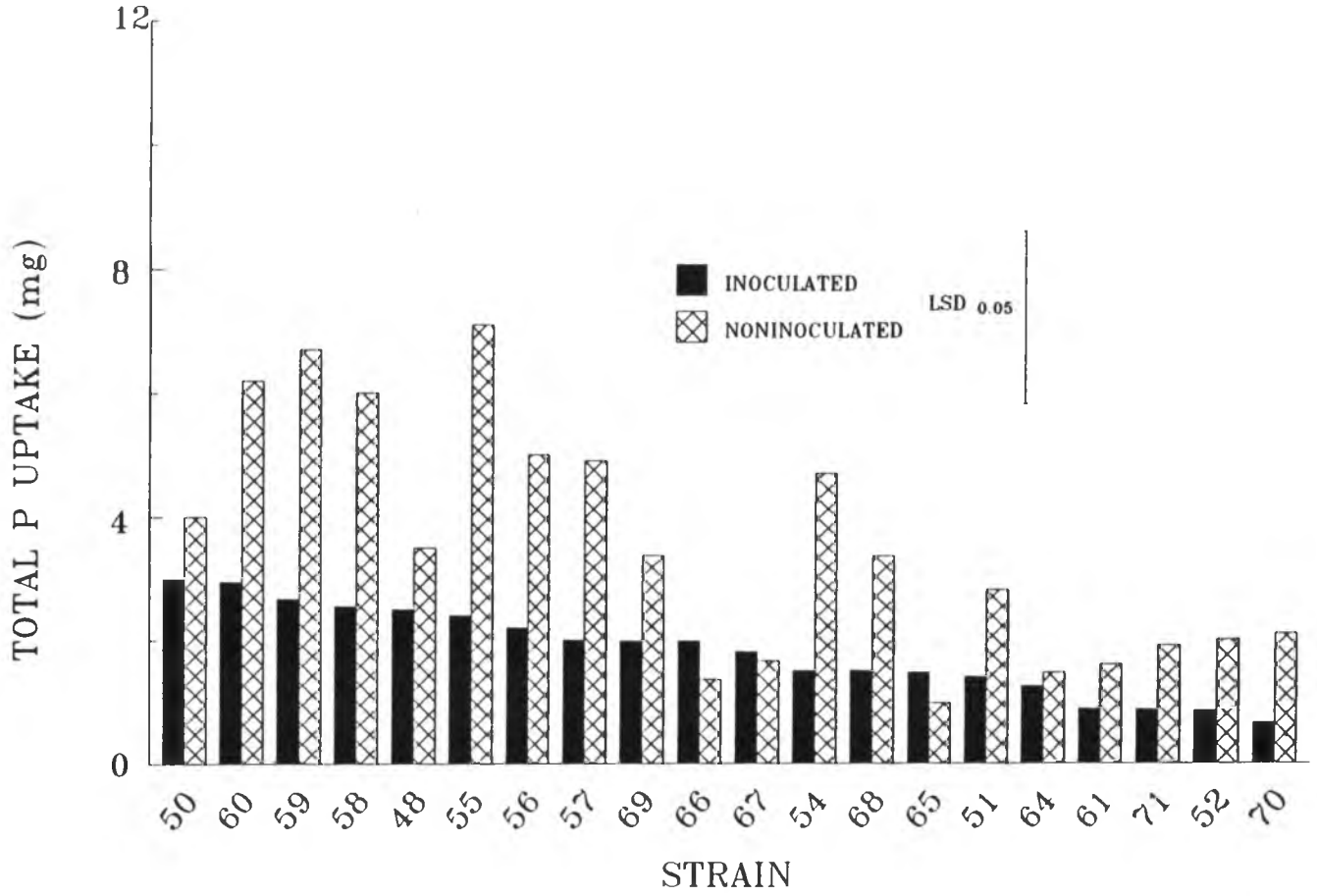

Fig. 2.3. Total P uptake of 20 tomato strains as a result of inoculation or noninoculation with mycorrhizae at the low P level (0.03 mg P/liter of soil solution) in Experiment 1.

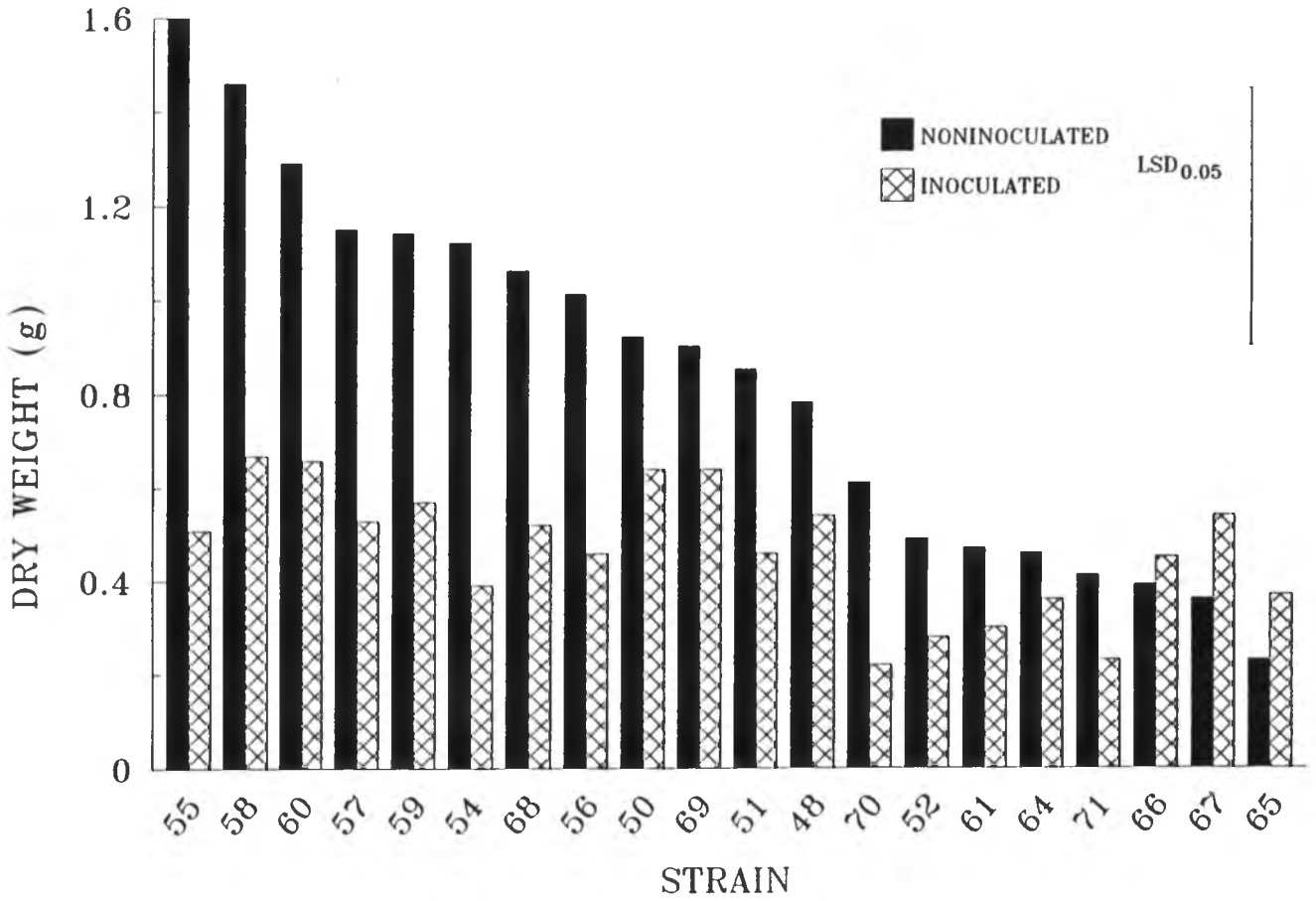

Fig. 2.4. Dry weight accumulation of 20 tomato strains as a result of inoculation or noninoculation with mycorrhizae at the low P level (0.03 mg P/liter of soil solution) in Experiment 1.

increased P uptake by mycorrhizal symbiosis, the P uptake was still too low to allow them to grow as well as most of the other stains under nonmycorrhizal condition. However, even the increased P uptake due to the mycorrhizal symbiosis with these strains was too low to allow them to grow as well as most of the other nonmycorrhizal plants.

Hayman (1982) also found that mycorrhizal plants briefly appeared smaller than the nonmycorrhizal controls around 1-2 weeks after inoculation. This early stage of growth depression did not carry through to later stage. Cooper (1975) found that mycorrhizae depressed plant growth at an early growth stage, but increased plant growth at a later stage in Leptospermum and Solanum spp. O'Bannon et al. (1980) found that mycorrhizae began to increase plant growth 21 days after inoculation. In the present experiment, 24 days of growth after inoculation apparently was not sufficient time for mycorrhizae to express their beneficial effects.

EXPERIMENT 2 - DETERMINATION OP APPROPRIATE PHOSPHORUS LEVELS TO SCREEN TOMATO VARIETIES

MATERIALS AND METHODS

Responses to soil P levels did not provide useful levels for screening in the first pot experiment. Therefore, a well-characterized low-P-tolerant strain, strain 159 (Coltman et al., 1985), was used in a second experiment to determine appropriate external P levels for screening tomato strains. Tomato seeds were surface sterilized by soaking in 1% sodium hypochlorite for 5 minutes and then planted in perlite. The perlite was soaked in Hoagland's solution to provide moisture and nutrients for seedling growth (Hoagland and Snyder, 1933). Ten days later the second true leaf had emerged and the seedlings were transplanted into pots.

The medium was 1:1 (by volume) of Waialua clay soil (Vertic Haplustoll) and basaltic sand. Each pot contained 1120 g of the soil/sand mixture. The phosphate-P concentration in the soil solution was 0.01 mg/liter before adding P. Eight levels of treble superphosphate were added (0, 6.6, 13.2, 19.8, 26.4, 33, 39.6, 46.2 g/kg of medium). The soil was equilibrated during 3 dry/wet cycles over a 15-day period. The soil solution concentrations after

equilibration are presented in Fig. 2.5. Potassium nitrate at 30.7 g per kg of medium was added at transplanting followed by two applications of 100 ml of 500 KNO_3 mg/liter during the 10th and 17th day after transplanting.

The pots were randomly arranged on a green house bench at the University of Hawaii, Manoa campus. Maximum and minimum average daily temperature was 43.5°C and 24°C, respectively.

Plants were harvested on May 31, 1987, 24 days after being transplanted into pots. Plant dry weights were recorded and tissue P concentrations were determined colorimetrically after dry-ashing at 550°C (Murphy and Riley, 1962).

The experiment was installed as a completely randomized design with 8 levels of soil phosphate and 6 replicates.

RESULTS AND DISCUSSION

Dry weight accumulation was greatest at 0.026 mg/liter soil solution P (Fig. 2.6) and dropped at higher soil solution P levels. The observed growth inhibition probably was caused by P toxicity. However, the growth depressions at 0.047 and 0.066 mg/liter level were more severe than at the 0.082 and 0.086 levels, indicating that growth was not inhibited by the high P concentrations alone. The reasons

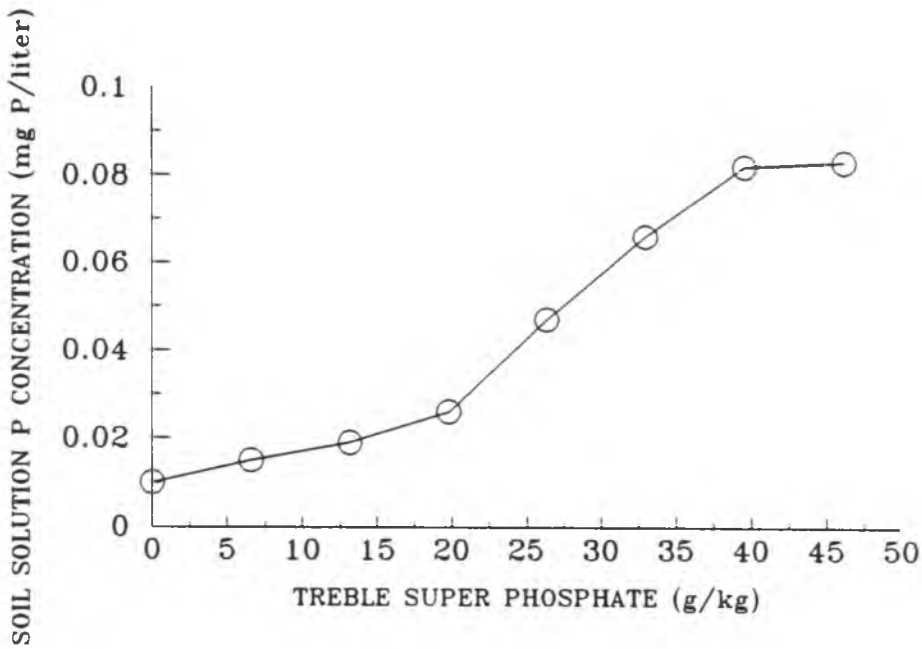

Fig. 2.5. The soil solution P concentrations at eight levels of treble super phosphate.

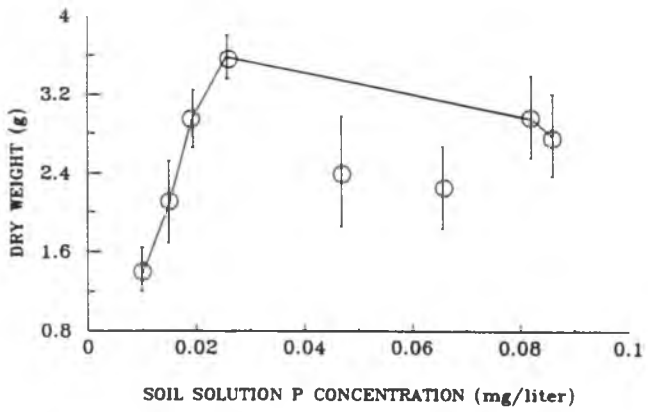

Fig. 2.6. Plant dry weights of tomato strain 159 at eight levels of soil solution P.

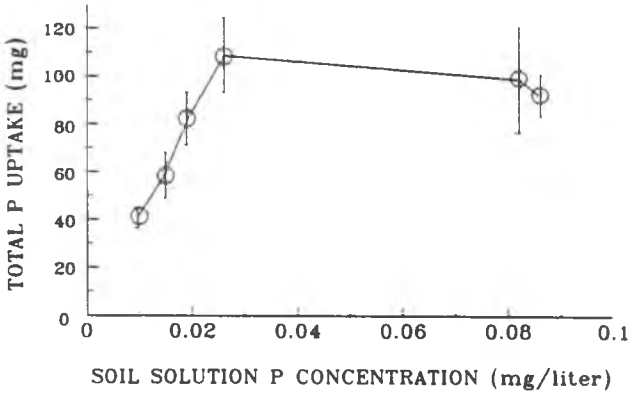

Fig. 2.7. Plant total P uptake of tomato strain 159 at six levels of soil solution P.

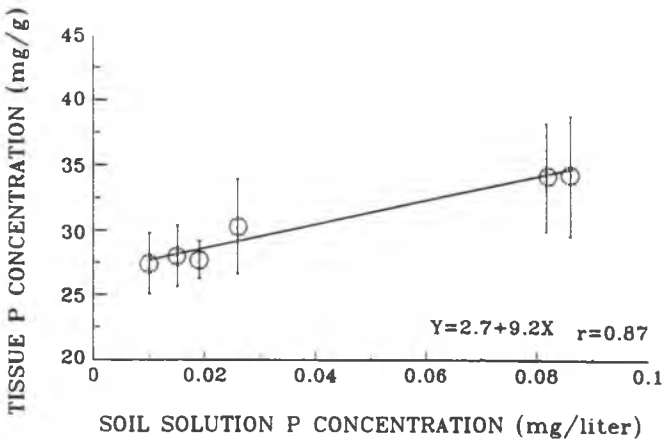

Fig. 2.8. Tissue P concentrations of tomato strain 159 at six levels of soil solution P.

for this strong growth inhibition at these two levels of P are unknown, but it did not appear reasonable to include these data in the regression analysis. Nevertheless, it still was difficult to fit a reasonable equation to the remaining data.

Total P accumulation was highly correlated to plant dry weight production (r=0.87), indicating that P availability was a primary factor limiting growth (Fig. 2.7). Tissue P concentrations were linearly related to soil solution P concentration (Fig. 2.8) as well. However, plant growth seemed limited by the high tissue P concentration. Tissue P concentration higher than 0.4 mg/g seemed to cause P toxicity.

In this experiment small increases in concentration of soil solution P in the soil test dramatically increased plant growth. The available P may have been greater than predicted from the soil test. The added treble superphosphate might not have been completely dissolved during the in-pot-equilibrating period and therefore may have released significant amounts of P during the experiment. In the soil test, the undissolved P would release during the process of soil P extraction, and then be absorbed on the soil surface due to the high buffer capacity. Consequently the equilibrium P concentration

might be very low. Phosphorus dissolving in the pots during active root growth may have been intercepted by the roots before having the opportunity to equilibrate with the soil.

Because of the uncertainty in the extent to which the P fertilizer dissolved in the soil solution, the optimal P soil solution for growth could not be determined. However, knowledge of the soil P concentration level for optimal growth was not considered essential, since later experiments followed identical procedures to this experiment, i.e., the soil was collected in the same field, determined to have similar original soil solution P concentrations by the same extraction method (Foy and Kamprath, 1970); it was fertilized with the same amount of treble superphosphate and equilibrated for the same period of time. Therefore, the added treble superphosphate should have provided similar amount of available P for plant growth in subsequent experiments as in this experiment. Because the treatment receiving 19.8 g of treble superphosphate per kg of medium (0.026 mg/liter soil solution P) gave the highest dry weight (Fig 2.6), and appeared to represent the level associated with maximum growth, it was selected as the "high P level" for subsequent screening experiments. The no-phosphate-added treatment (0.01 mg/liter soil solution P) was selected as the low P level for the following experiments.

EXPERIMENT 3- SCREENING FOR LOW-P TOLERANT STRAINS

MATERIALS AND METHODS

Twenty-tree tomato strains (Fig. 2.9) were screened for growth at low and high levels of P as determined in Expt. 3. The strains came from the same sources as those used in Expt. 1; plant introduction numbers and origins of these strain are presented in the Appendix B.

The tomatoes seeds were germinated in a perlite-nutrient solution and seedlings were transplanted to pots 10 days after sowing. The procedure was the same as that in Expt. 2.

The soil P level was 0.01 and 0.027 mg/liter before the experiment, and 0.008 and 0.024 mg/liter at the end of the experiment. One hundred ml of KNO_3 (500 mg/liter) was added at the 10th and 17th day after transplanting.

The experiment was conducted in August, 1987 in the same greenhouse as Expt. 2. Maximum and minimum daily average temperatures were 42.6^{o}C and 23.2^{o}C respectively.

The experiment employed a completely randomized design, with two levels of soil phosphate and six replicates.

RESULTS AND DISCUSSION

In this experiment, plant growth was reduced 70 to 87%

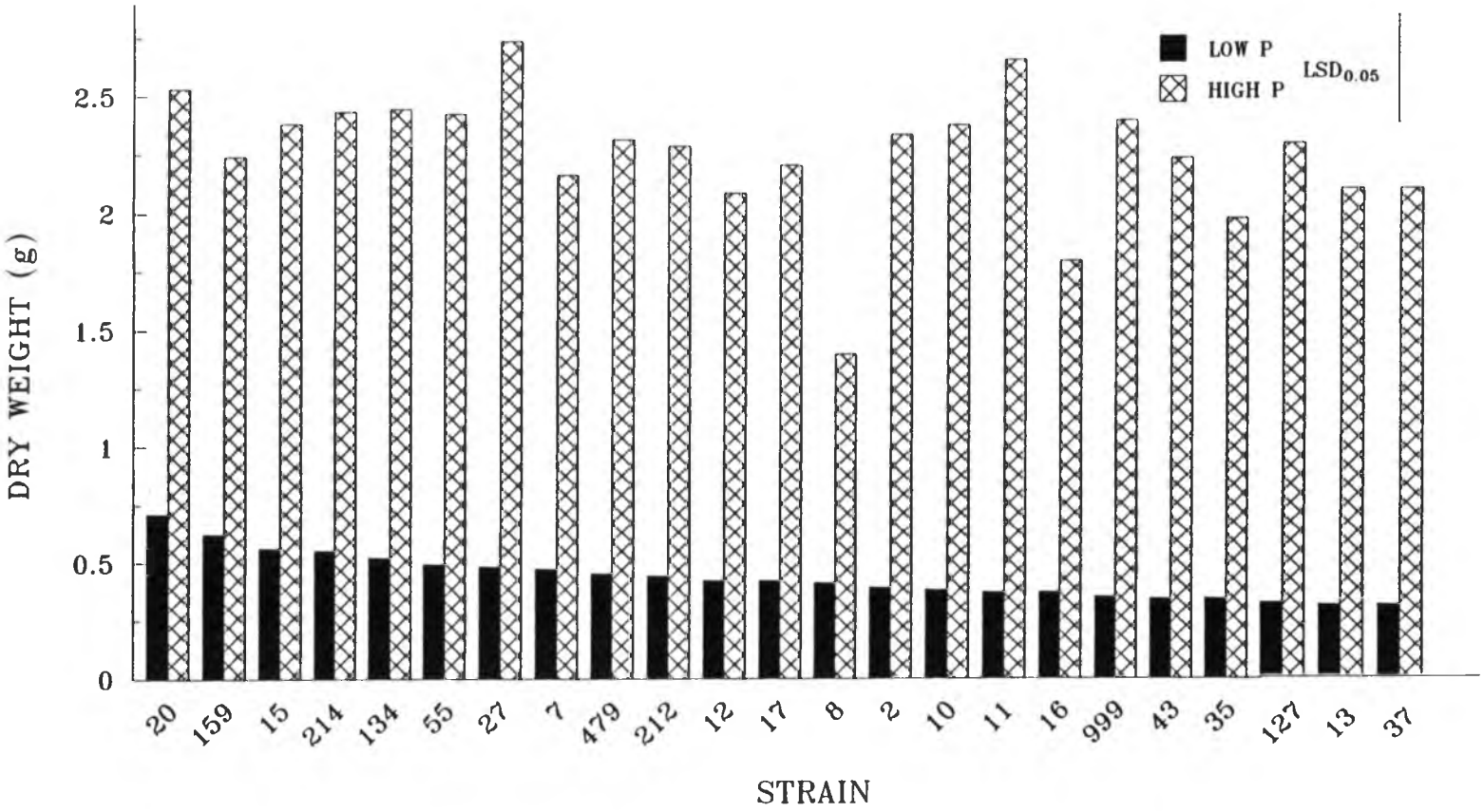

Fig. 2.9. The dry weight accumualtion of 23 tomato strains at low (0.01 mg/liter) and high (0.027 mg/ liter) soil solution P concentrations in Experiment 3.

at low P level relative to the high P level (Fig. 2.9). This showed that 0.01 mg/liter (low P) was an effective level to cause P stress, enabling identification of P tolerant strains. Because of the high variation in the data, the LSD test could not be used to separate the strains' low-P tolerance. Therefore, the strains that had lowest and highest dry weight ratio (low P dry weight/ high P dry weight) were selected as tolerant and intolerant strains. Strains 8, 20, and 159 which had highest dry weight ratio were identified as low-P tolerant strains (Fig. 2.10) and strains 43, 13, 37, 999, 11 and 127 which had the lowest dry weight ratio were selected as the low-P tolerant strains (Fig. 2.10).

In this study all of the strains at both low and high P levels had low tissue P concentrations. The tissue P concentrations ranged from 2 to 2.6 mg P per gram dry weight at the high P level and from 1-2 mg P per gram dry weight at the low P level (Fig. 2.11). However, 25-day-old tomato plants should have between 5-8 mg P per gram dry weight tissue under sufficient soil P condition and between 2-3 mg P under moderate P deficient condition (Coltman, personal communication). Therefore, the plants in this study may have suffered P stress at both high and low P levels.

The plant P efficiency was commonly measured by the

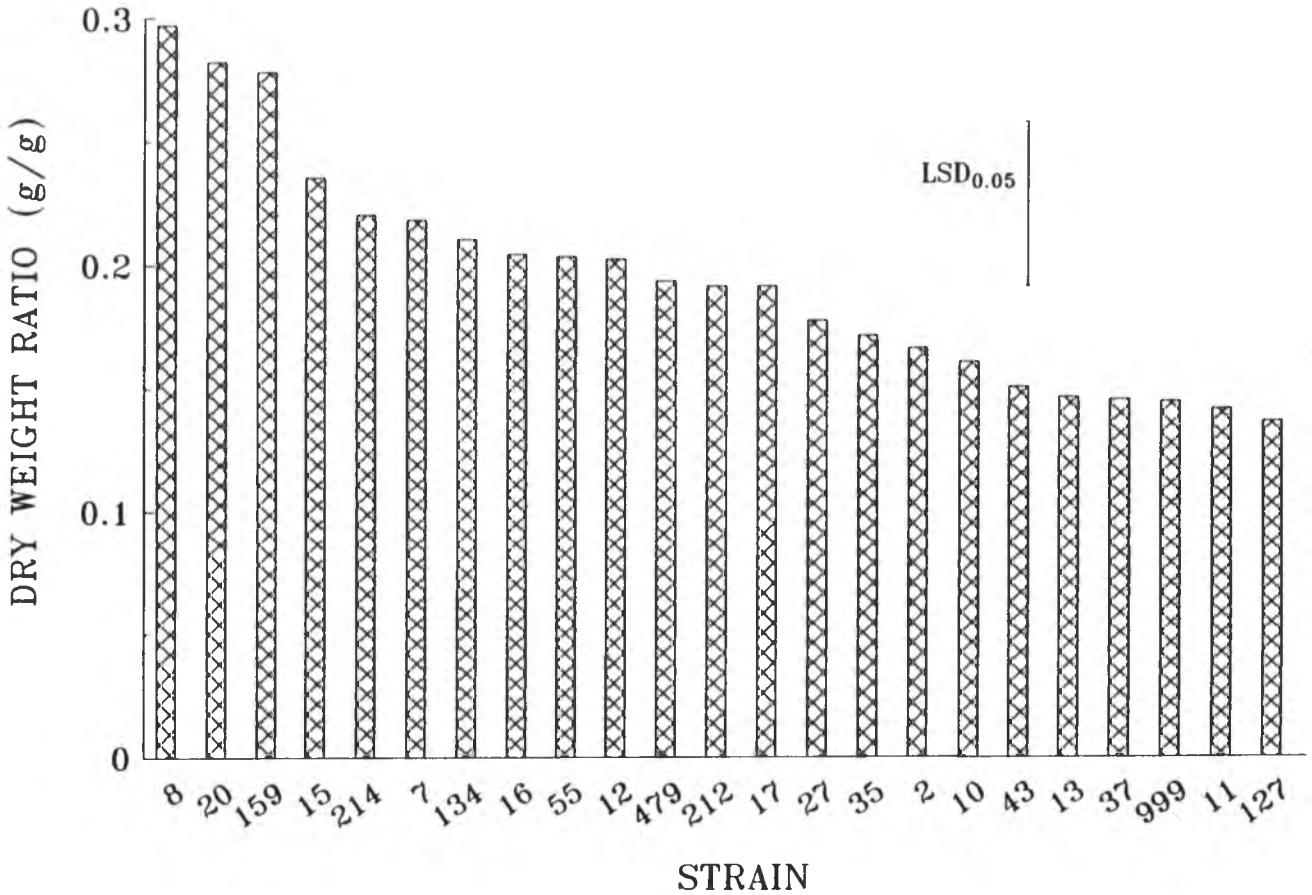

Fig. 2.10. The dry weight ratio (low P dry weight/ high P dry weight) of 23 tomato strains in Experiment 3.

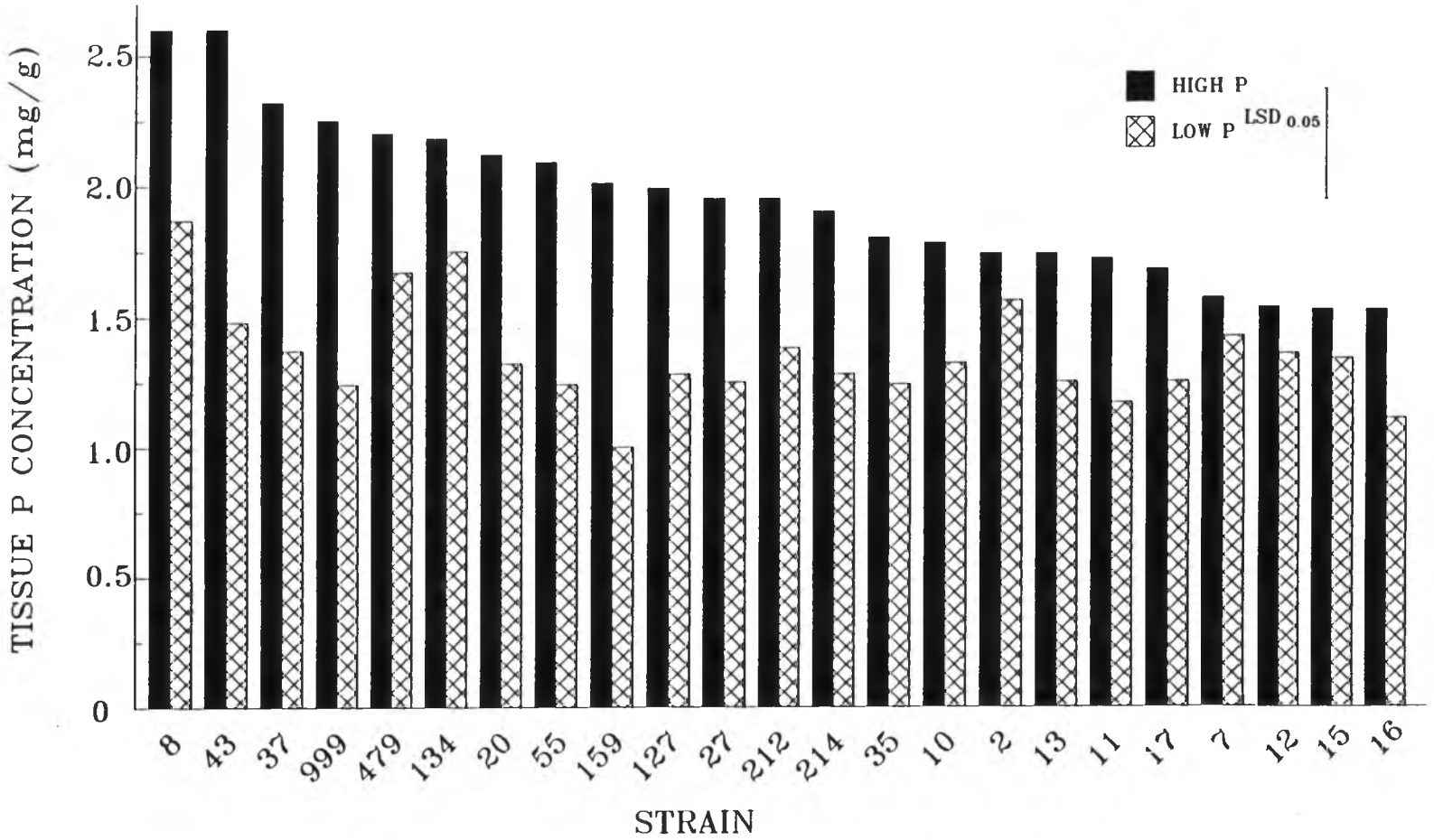

Fig. 2.11. The tissue P concentrations of 23 tomato strains at low (0.01 mg/ liter) and high (0.027 mg/ liter) soil solution P concentrations in Experiment 3.

total P uptake and internal P utilization efficiency. The internal P utilization efficiency (PUE) was calculated by dry weight divided by P uptake. Coltman et al. (1985) showed that both high P uptake ability and PUE at P deficient condition contributed to tomato strains' low-P tolerant ability. However, in this experiment, PUE was not highly correlated with dry weight accumulation in the low P treatment ($r=0.35$) and did not seem to be an important factor in low-P tolerance. Total P uptake was highly correlated with dry weight ($r= 0.9$) under the low P treatment. Therefore, the P uptake ability under the P deficient conditions might be the most important factor that affected the plant growth under the P deficient condition.

Comparing tolerant and intolerant strains which have similar dry weight accumulation at high P levels might help to understand P tolerant mechanisms under the P deficient condition (Table 2.1). All tolerant strains had higher P uptake than the intolerant strains. In addition, strain 159 had significantly higher P utilization efficiency than the other strains. Phosphorus utilization efficiency partially contributed to the high low-P tolerant ability of strain 159.

Table 2.1. Dry weight, total P uptake and P utilization efficiency of low-P tolerant and intolerant tomato strains at 0.01 mg P/liter soil solution (low P level).

STRAIN	DW[y] (g)	TPU[z] (Mg)	PUE[w] (g/Mg)	HP-DW[u]
20 t[x]	0.71 a	9.69 a	0.77 b	2.50 a
159 t	0.62 a	6.07 bc	1.01 a	2.25 a
15 t	0.56 a	7.02 ab	0.75 b	2.35 a
214 t	0.55 a	7.02 ab	0.79 b	2.40 a
999 i	0.35 b	4.25 bc	0.85 b	2.40 a
43 i	0.34 b	5.16 bc	0.70 b	2.30 a
127 i	0.29 b	3.72 c	0.80 b	2.35 a
mean	0.49	6.14	0.81	2.33
CV	36.5%	42.4%	16.6%	30.0%

[x] t & i= tolerant strain and intolerant strain.
[y] DW = total plant dry weight at 0.01 mg P/ liter soil solution P.
[z] TPU = total P uptake at 0.01 mg P/ liter soil solution.
[w] PUE = P utilization efficiency (mg DW produced per mg P absorbed).
[u] HP-DW = total plant dry weight at 0.027 mg P/ liter soil solution P.
[v] Means of followed by the same letter are not statistically different according to Fisher's 'protected' $LSD_{0.05}$.

CONCLUSION

Strains 50, 51, 55, 58, 59, 60, 68 and 69 and strains 15, 20, 159 and 214 were identified as low-P-tolerant strains in Experiments 1 and 3, respectively. However, one must be cautious when drawing conclusions about the ability of plants to take up P from screening studies with young plants. Plants have different P uptake abilities during different stages of growth (Fox et al., 1974). These studies only examined the first 24 days of tomato vegetative growth in a pot and these results may not be indicative of fruit productivity. Comparing vegetative and reproductive stages is necessary. Further more, these experiment were conducted in small (900 ml) pots. Limited space for root growth may affect roots' extension and phosphate uptake. To verify these pot study results, the strains need to be evaluated in the field.

Mycorrhizae frequently depressed host plant growth in the first few weeks after inoculation. This early stage of growth depression may not carry through to later growth stages. This small pot screening method only allowed 24 day of plant growth and was not suitable for observing the mycorrhizae-host interaction. Screening mycorrhizal response requires a long growth period and a big pot to support plant growth. However, handling the big pots were

inconvenient and conducting the study in field may be more suitable than in the pots.

CHAPTER 3 The FIELD STUDY

INTRODUCTION

In order to screen a large germplasm collection with minimal cost and space, many studies have evaluated plants for low-P tolerance during the vegetative growth stage (Fawole et al., 1982; Coltman et al., 1983). However, data derived from screening tomato cultivars during vegetative growth must be interpreted with caution. Fox et al. (1974), for example, found that corn required 0.2 ppm P in solution during early growth, but only needed 0.06 ppm P during grain fill. Tomato strains could vary in their P requirements at different stages of growth in different ways. Thus, conclusions about the yielding ability of tomatoes may be better drawn when evaluating P tolerance during fruit set.

Greenhouse studies have given misleading results in predicting low-P tolerance. Caradus et al. (1986) found a poor correlation for differentially P tolerant strains of white clover compared in greenhouse and field studies. Fox and Kamprath (1970) also noticed marked differences in wheat strain performance between pot and field experiments. They suggested that P movement in soils may have caused some of this disparity. In the soil, phosphate moves primarily by diffusion, along a concentration gradient. In pots with

dense root mats, P interception by the roots plays the more important role in uptake. Pot walls limit root expansion and thereby may bias results against plants that achieve P uptake efficiency via vigorous root production.

Mycorrhizal fungi form symbiotic associations with a wide range of agriculturally important crops. The main benefit of mycorrhizal infection is increased P uptake, particularly in plants growing in low P soils (Yost and Fox, 1979). The speed and extent of colonization, however, can differ between strains (Azcon and Ocampo, 1981). Differential interactions between mycorrhizae and strains may be important in selecting for P efficiency.

The objectives of this study were: (1) to screen tomato strains for P tolerance during fruit set and under field conditions, and (2) to evaluate the effect of mycorrhizal symbiosis on plant P uptake and differential low P tolerance among strains.

MATERIALS AND METHODS

The field for the tomato screening experiment was prepared at the Waimanalo Research Station, University of Hawaii. The soil was classified as a Waialua clay (Vertic Haplustoll), pH 6.1. Four years previously, the field had been divided into eight subplots and fertilized with two

levels of treble superphosphate to achieve soil solution P levels of 0.03 and 0.3 mg P per liter soil solution respectively. Six months prior to planting this experiment, the soil P levels were tested again, and found to be 0.03 and 0.3 mg P for the low and high P treatment, respectively. Since P is immobile in the soil, and no crop was grown in the field after the test, the soil P levels were deemed appropriate for this screening experiment, and no further adjustment in P levels was attempted. Unfortunately, during the six months prior to planting this experiment the P levels appear to have changed considerably. After transplanting, the solution P concentrations of high P and low P plots were found to be 0.031 and 0.008 mg/liter P, respectively. These levels were calculated by desorption in 0.01 M $CaCl_2$ (Fox and Kamprath, 1970). Soil solution P levels after the experiment were 0.03 at the high P level and 0.0035 mg/liter P at the low P level. No potassium was applied since a soil test revealed adequate amounts in the soil. Ammonium sulfate was broadcast and incorporated during rotovation to provide 220 kg N/ha. The field was fumigated with 1 kg methyl-bromide/chloropicrin per 25 m^3 soil.

Twenty-three strains from Expt. 3, and 8 strains from Expt. 1 were evaluated in this field study. The tomato

transplants were raised in the Agronomy greenhouse, University of Hawaii. The plants were grown in a medium consisting of 1:1 sphagnum peat : vermiculite (by volume), adjusted to pH 6.3 with dolomitic lime. Micronutrients were supplied as 0.5 kg/m^3 micromax (Sierra chemical Co., Milipitas Calif.). Osmocote (19N-2.6P-10K Sierra chemical Co., Milipitas Calif.) at 10 kg/m^3 served as the macronutrient source, providing 1.9 kg N, 0.026 kg P and 1 kg K per m^3.

Thirty-day-old tomato seedlings were transplanted into the field. Tomatoes were planted in the center of 150 cm wide beds. The plants were spaced 60 cm between plants and 3 plants of the same strains were planted in each plot. The middle plant was harvested as the sample. To decrease the likelihood of contamination, 5 plants was planted between the inoculated and noninoculated treatments. Plants were irrigated by trickle irrigation.

Inoculated plants received 300 spores of VAMF (Glomus aggregatum) suspended in 10 ml of deionized water when the seedlings were transplanted into field. To determine if contamination occurred in the soil, 24 root samples were randomly taken from the field 2 months after transplanting. Twenty root pieces (1 cm long) were stained (Phillips and Hayman, 1970) and examined for mycorrhizal colonization.

None of the 18 noninoculated root samples tested contained mycorrhizae, while all of the 6 mycorrhizal inoculated root samples showed mycorrhizae infection. The noninoculated treatments, thus, were assumed to be free of mycorrhizae.

A silver-black plastic mulch was used as the main plot in a split-split-split plot design. However, no significant main effects nor interactions with other treatments were found using plastic mulch. Therefore, the mulch treatment will be ignored in the later discussion. The experiment was analyzed as a 2x2x32 (soil solution P x mycorrhzial inoculation x strains) split, split plot design with soil solution P as the mainplot, mycorrhizal inoculation as the subplot, strains as the sub-subplot.

The harvest period for each strain lasted 15 days, beginning 70 days after transplanting for the earliest maturing strain. Because the strains matured at different rates, an effort was made to harvest the early strains first, and the slow maturing strains last. The initiation of harvesting proceeded as follows: (1) small-fruit (about 3 cm diameter) strains were harvested when the plants had an average of 30 ripen fruits; (2) medium-fruit strains (about 5 cm diameter) were harvested when the plants had an average of 15 ripen fruits, and (3) big-fruit strains (about 7 cm diameter) were harvested when the plants had an average of

10 ripe fruits. From each plant the stem, leaf, green fruit, and ripe fruit fresh weights and dry weights were recorded. From each treatment, one tomato stem (from the first branch to the apical meristem), 8 ripe fruits and 8 green fruits were sampled to determine P concentrations in the stem, leaves, and fruit (ripe and green). Tissue P concentrations were determine by the molybdenum blue method (Murphy and Riley, 1962). The fresh weight/dry weight ratios and tissue P concentrations from samples of shoots (fruit not included) ripen fruit, and green fruit were used to estimate total P uptake of the strains.

RESULTS AND DISCUSSION

P effects:

The plant dry weight ratio (dry weight at low P/ dry weight at high P) was not used as a parameter to identify P tolerant strains in this study. Plant dry weight consisted of stem and fruit weight. The ratio of stem to fruit varied noticeably among strains and among P levels (Appendix B). Because of this high variability no standardization criteria could be determined by which to compare different strains using dry weight. Therefore, the P uptake ratio (P uptake at low P/ P uptake at high P) was used to evaluate low P tolerance among the strains. In order to adjust for

differences in harvest date, total P uptake of plant was divided by days in the field as daily P uptake (P uptake/ day).

Due to the high variation in the data, P uptake ratio of strains were not significantly different in Lest Significant Difference (LSD) at 5% level. The low-P tolerant strains cannot identify by LSD at 5% level. Therefore, the strains had the highest and lowest P uptake ratio were identified as the tolerant and intolerant strains. Strains 59, 999 and 43 had the highest daily P uptake ratio (Fig 3.1) and were identified as the most low P tolerant strains. Strains 8 and 212 which had the lowest daily P uptake ratio (Fig. 3.1) were identified as low P intolerant strains.

The daily P uptake correlated highly with P accumulation in the fruit ($r=0.93$, $P<0.01$). However, the daily uptake had a lower correlation with fruit yield ($r=0.66$, NS). A possible cause for this low P correlation may be related to different fruit P utilization efficiencies of the strains (Table 3.1). The fruit P utilization efficiency of a plant is defined as the amount of fruit dry weight produced per gram of phosphorus in the fruit. The fruit P utilization efficiencies ranged from 250 mg dry tissue per mg P to 530 mg dry tissue per mg P. If the

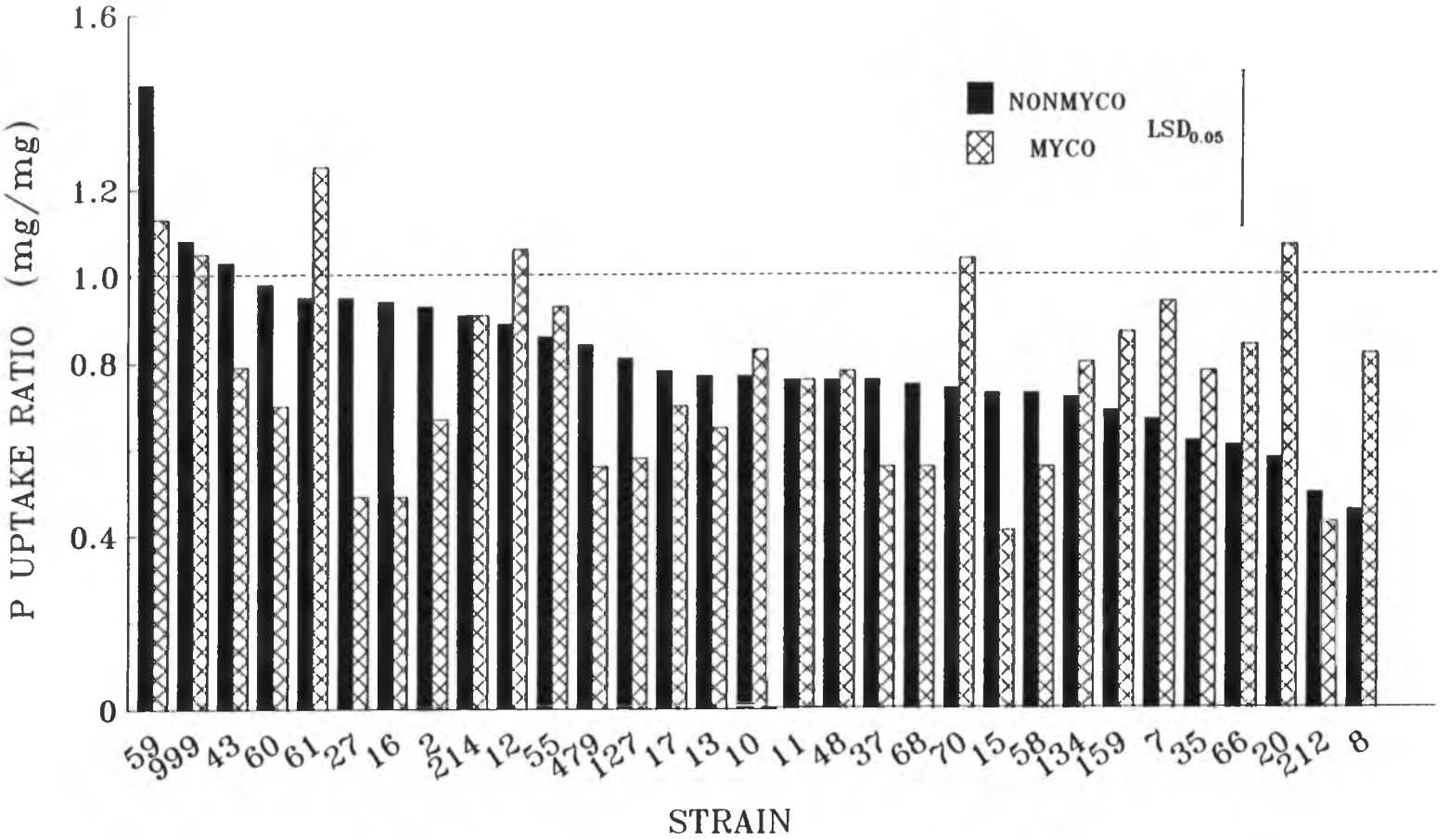

Fig. 3.1. The P uptake ratio (P uptake at low P /P uptake at high P) of 31 strains tomato strains inoculated and noninoculated with mycorrhizae.

Table 3.1. The fruit P utilization efficiency of 31 tomato strains at the low (0.008 mg P/liter soil solution) and high (0.03 mg P/ liter soil solution) P levels in the field study.

	FRUIT P UTILIZATION EFFICIENCY[x]	
STRAIN	low P	high P
2	249.96	251.46
7	412.60	333.25
8	265.71	266.34
10	419.14	374.94
11	381.18	363.28
12	307.94	306.37
13	251.79	201.61
15	530.43	311.82
16	451.43	431.10
17	406.03	380.42
20	438.68	284.86
27	258.37	216.89
35	272.76	270.24
37	331.85	198.61
43	305.44	296.77
48	453.90	278.72
55	525.37	344.16
58	367.24	358.12
59	315.95	381.76
60	260.93	258.42
61	464.66	354.01
66	388.33	416.73
68	494.77	400.96
70	418.60	302.27
127	414.75	402.46
134	327.51	272.61
159	363.19	325.19
212	463.06	381.72
214	374.47	389.47
479	401.62	385.18
999	371.29	373.76
MEAN	398.27	368.89

[x] FRUIT P UTILIZATION EFFICIENCY, milligrams of fruit dry weight per mg P.

characters of high fruit P utilization efficiency can be transferred into the low-P-tolerant strains, this would help to achieve high productivity with minimum P depletion from the soil and help to preserve the limited soil P fertility.

Interestingly, strain 59 was much more efficient in taking up P under low P conditions (increasing 30%) than under the high P treatment (Fig.3.2). This increased uptake was reflected in a significantly higher fruit yield at the low P level than at the high P. Strain 59 also grew better under low P conditions in the pot study of Expt. 1. Strain 59, however, was the exception. Most strains increased P uptake as P concentrations in the soil improved (Fig. 3.2).

Comparing tolerant and intolerant strains which have similar daily P uptake at high P levels might permit elucidation of the low-P tolerance mechanisms operating under the P deficient condition. Seven strains were selected using this criterion (Table 3.2). The strains had various PUE. However, the high PUE was not the main mechanism that contributed to high dry weight accumulation, but the high total P uptake. For example, the strains 7, 66, 159 and 999 had very similar dry weight at the high P level and very different dry weight accumulation at the low P level. Strain 999 had significantly higher dry weight than the other strains. This is not due to superior PUE,

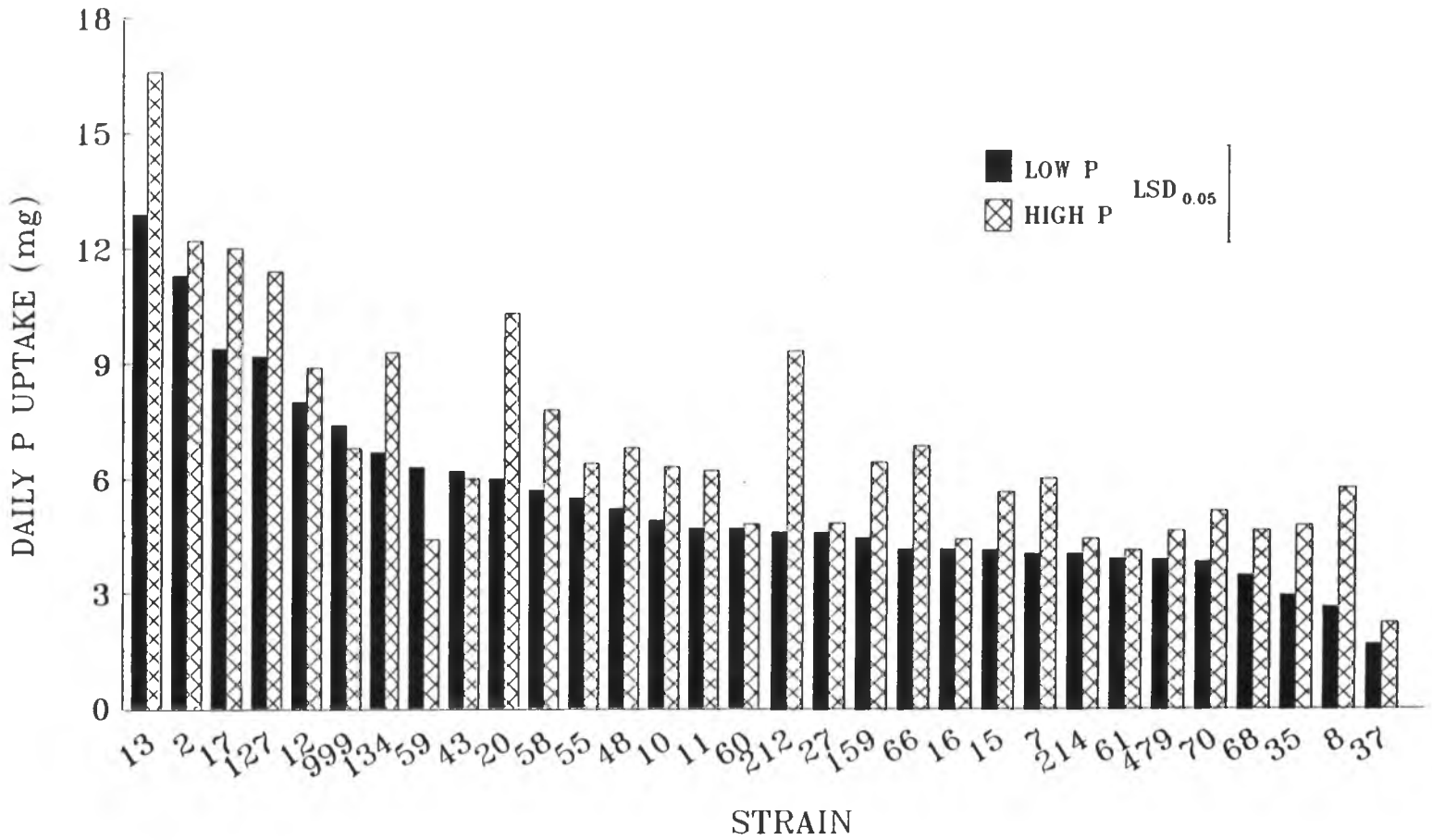

Fig. 3.2. Daily P uptake of 31 tomato strains at high P (0.03 mg P/liter soil solution) and low P (0.008 mg P/liter soil solution).

Table 3.2. Comparison of P uptake, P uptake ratio (low P/ high P P uptake), dry weight, dry weight ratio (low P/ high P dry weight), and P utilization efficiency of nonmycorrhizal tomato strains at low (0.008 mg P/liter soil solution) and high (0.031 mg P/ liter soil solution) P levels.

	NONMYCO. DAILY P UPTAKE[z] (mg)			NONMYCO. DRY WEIGHT[w] (g)			NONMYCO PUE[y]	
STRAIN	high P(H)	low P(L)	L/H ratio	high P(H)	low P(L)	L/H ratio	low P	high P
7	6.06 a[x]	4.07 bc	0.67 bc	3.69 a	2.80 bcd	0.76 c	683.1	614.3
8	5.80 a	2.69 c	0.46 c	2.49 c	1.30 d	0.52 c	480.1	428.9
43	6.04 a	6.21 ab	1.03 a	2.52 c	2.80 bcd	1.11 ab	449.2	416.5
55	6.41 a	5.53 ab	0.86 ab	2.77 bc	3.32 abc	1.20 a	597.1	432.4
66	6.90 a	4.20 bc	0.61 bc	3.75 a	2.09 cd	0.56 c	496.7	544.4
159	6.48 a	4.50 b	0.69 bc	3.55 a	2.92 bc	0.82 bc	667.6	549.3
999	6.84 a	7.37 a	1.08 a	3.17 ab	3.73 a	1.18 a	507.8	460.2
mean	6.34	4.94	0.88	3.11	2.95	0.77	554.6	492.3
CV	17.6	24.5	25.3	18.57	25.75	23.9		

[x] Means followed by the same letter are not statistically different according to Fisher's 'protected' $LSD_{0.05}$.
[y] PUE = P utilization efficiency (mg dry weight produced per mg P uptake.
[z] Includes P accumulation in stems, leaves and fruit devided by days of growth.
[w] Includes dry weight accumulation in stems, leaves and fruit devided by days of growth.

but the higher P uptake ability at the low P level than the other three strains.

Mycorrhizal effects

Plants that develop symbiotic associations with mycorrhizae frequently take up more phosphorus and yield better than plants without mycorrhizae (Mosse, 1973, 1977). However, in this experiment mycorrhizae effects were strain specific. The ANOVA table (Table 3.3) indicated a highly significant interaction between strains, soil P, and mycorrhizae inoculation.

Phosphorus uptake ratios of mycorrhizal vs nonmycorrhizal plants at the two P levels were evaluated to determine the mycorrhizal effect on P uptake (Fig. 3.3). Mycorrhizal inoculation increased P uptake more than 100% for strains 16, 68, and 479 at the high P level. At the low P level, P uptake of strains 7, 20, 68, 70 and 479 was increased 35% by mycorrhizal inoculation. However, P uptake in strains 8, 66 and 134 was reduced by over 20% compared with that in noninfected plants at high P levels. The P uptake in strains 17 and 27 were also decreased more than 30% by mycorrhizal inoculation at the low P level. Mycorrhizae may have competed with the plant for limited P available in the soil or limited carbohydrates in the plant.

Table 3.3. The ANOVA for 31 tomato strains grown at two soil P levels with and without mycorrhizal inoculation in the field study.

Source of variation	df	
Soil P (P)[y]	1	**[x]
Inoculation (I)[z]	1	NS
Strain (S)	30	**
P x I	1	NS
P x S	30	**
I x S	30	**
P x I x S	30	**

[x] ** significant at 1% level.
* significant at 5% level.
NS non-significant.
[y] Soil P = soil solution P concentration of 0.008 mg/liter or 0.031 mg/liter.
[z] Inoculation = mycorrhizal inoculated versus non-inoculated.

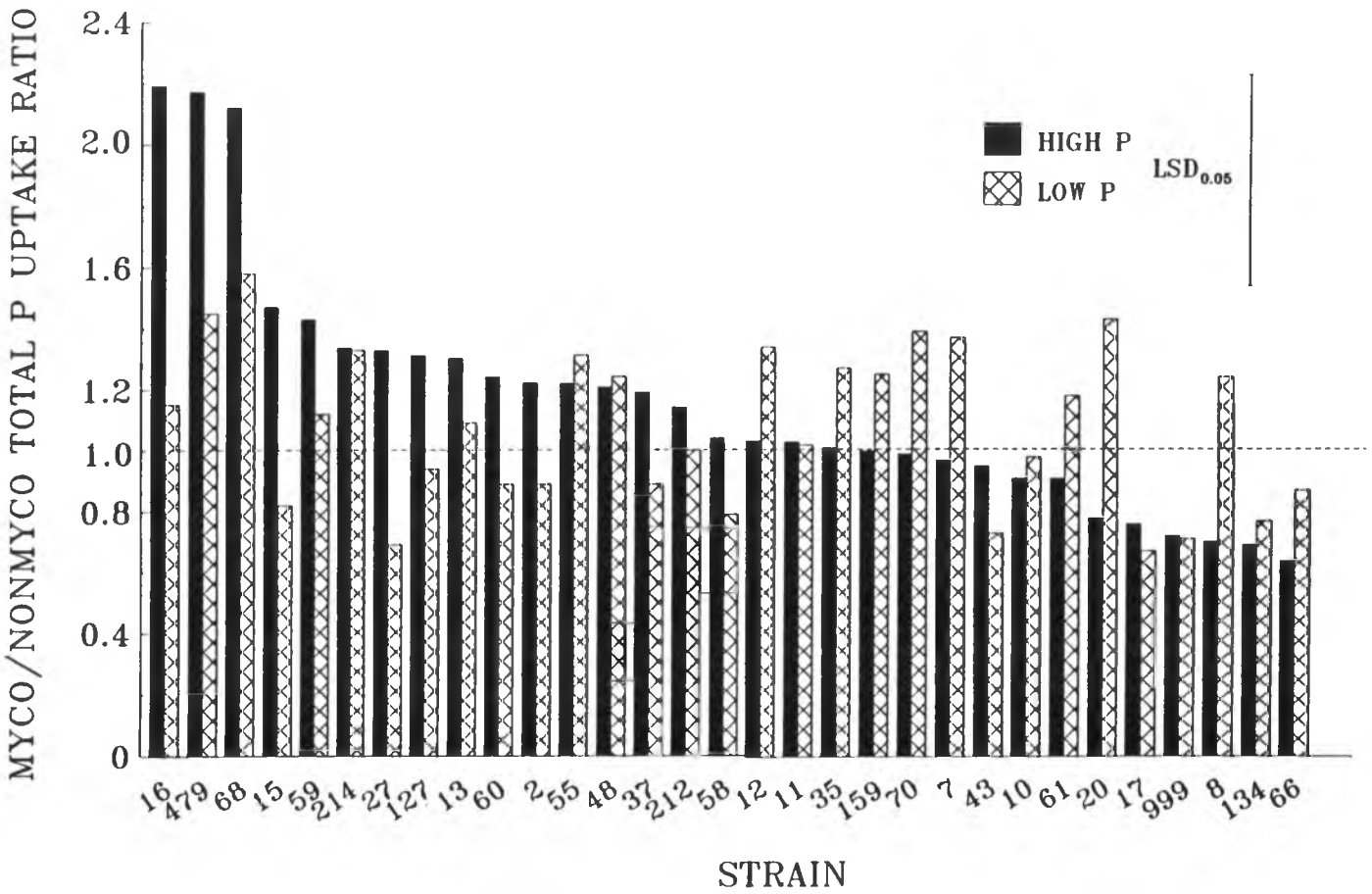

Fig. 3.3. The effect of mycorrhizal inoculation on total P uptake ratio of 31 tomato strains at high soil P (0.031 mg/liter soil solution)and low soil P (0.008 mg P/ liter soil solution).

This decrease was not significant because of the high variation in the data.

Mycorrhizal inoculation benefited strains which had low P uptake more than strains which had high P uptake. To illustrate this point, strains which had the highest myco/nonmyco total P uptake ratios were compared with strains which had the lowest ratios at both P levels (Table 3.4). With the exception of strain 20, strains with the high myco/nonmyco total P uptake ratio at low P (strains 8, 68, 70 and 479) had very low daily P uptake. The strain 20 which had P uptake higher than the average of 5.13 was a exception of high myco/nonmyco P uptake ratio strains. However, this strain had very low P uptake ratio (low P/high P P uptake at nonmyco condition) and showed severe P deficiency at low P level. At high P, all the strains that had my/nonmy ratios well above 1.0 (Strains 68, 479 and 16) also had daily P uptake lower than the average at high P. With the exception of strain 20, all of the strains that had higher than average P uptake had my/nonmy P uptake ratios below 1 at both the low and high P levels. However, strains with low P uptake ability did not necessary have my/nonmy P uptake ratios higher than 1 eg. strains 16, 27, and 66 at low P and strain 8 at high P. Furthermore, no trend was seen between mycorrhizal effects and tissue P concentration.

Table 3.4. Comparison of daily P uptake, P uptake ability (nonmyco low P/ high P P uptake) and tissue P concentration at low (0.008 mg P/liter soil solution) and high (0.031 mg P/ liter soil solution) P level for tomato strains especially responsive or unresponsive to mycorrhizal inoculation.

	Ratio of P uptake of myco.vs nonmyco. on total P		Daily P uptake[y] at nonmyco. (mg)		P uptake ratio (NONMYCO. L/H	Tissue P conc. mg P per g	
Strain	low P	high P	low P (L)	high P (H)	P UPTAKE)	low P	high P
8	1.24 a	0.70 c	2.69 f	5.80 cd	0.46 d	2.08	2.33
20	1.43 a	0.80 c	5.99 bcde	10.32 ab	0.58 cd	1.81	2.63
70	1.39 a	1.00 bc	3.86 ef	5.21 cd	0.74 abcd	2.39	3.31
68	1.58 a	2.12 a	3.52 f	4.69 cd	0.75 abcd	2.02	2.49
479	1.46 a	2.17 a	3.92 def	4.67 cd	0.84 abcd	2.49	2.60
16	0.85 abc	2.19 a	4.18 def	4.45 d	0.94 abc	0.92	1.56
27	0.69 c	1.33 b	4.63 cdef	4.89 cd	0.95 abc	3.87	4.01
17	0.67 c	0.66 c	9.39 a	11.99 a	0.78 abcd	2.46	2.63
66	0.89 bc	0.69 c	4.20 def	6.90 c	0.62 cd	2.58	2.40
134	0.77 c	0.64 c	6.72 bc	9.35 b	0.58 bcd	3.11	3.67
999	0.71 c	0.73 c	7.34 ab	6.84 c	1.02 a	2.69	2.68
mean	1.06	1.18	5.13	6.78	0.71	2.40	2.75

[y] Daily P uptake = total P uptake/harvest days

[u] Means of followed by the same letter are not statistically different according to Fisher's 'protected' $LSD_{0.05}$.

Because mycorrhizae selectively benefited low-P- uptake strains, inoculation strongly influenced the classification of low-P tolerant strains. The strains which had the highest P uptake ratios (P uptake at high P/ P uptake at low P) under nonmycorrhizal conditions were 59, 999, 43 and 60 (Fig.3.1). In VAMF infected soils, strains 61, 59, 20, and 12 had the highest P uptake ratio (Fig. 3.1). Thus, the presence or absence of mycorrhizae should be noted when making recommendations on low P tolerant strains.

However, P uptake was increased by mycorrhizal inoculation for most of the strains at both high and low P levels (Fig. 3.3). The inoculation resource of VAMF was very easy and cheap to produce for large scale field inoculation (Waterer et al., 1988). Therefore, the mycorrhizal inoculation may be considered as a valuable procedure for growing the tomato on P deficient soils. Screening for high mycorrhizal efficiency of low-P tolerant strains may be a very effective strategy to overcome the low productivity on soils with low levels of available P.

In order to further understand mycorrhizal effects on low P tolerance, the seven strains used previously for comparing low P tolerance mechanisms under nonmycorrhizal conditions were compared under mycorrhizal conditions (Table

3.5). Mycorrhizal inoculation did not significantly decreased PUE at both the high and low P levels. The PUEs of mycorrhizal and nonmycorrhizal plants were highly correlated at both P level ($r=0.75$, $P<0.05$ at low P level and $r=0.89$, $P<0.01$ at high P level). The correlation of daily dry weight and daily P uptake between mycorrhizal and nonmycorrhizal treatments was low at both high and low P level. Mycorrhizal inoculation also significantly changed the strain rankings for the low P/ high P dry weight ratio and P uptake ratio. Therefore, different conclusions about differences in low-P tolerance among the strains would be made depending on whether or not they were mycorrhizal.

Problems with the field study

After the experiment, soil solution P concentrations at high (0.031 mg/liter) and low (0.008 mg/liter) P levels were discovered to be much lower than the soil P concentrations originally planned (0.3 and 0.03 mg/liter for high and low P, respectively). However, the plant seemed only suffer slight P stress at both P level. Four strains that had been randomly selected and took leaf sample at the onset of flowering stage on the first fully extended young leaf. The tissue P concentration of these leaf samples was 2.7 to 3 mg P /g at the low P level and 3.2 to 3.3 at the high P level.

Table 3.5. Comparison of P uptake, P uptake ratio (low P/ high P P uptake), dry weight, dry weight ratio (low P/ high P dry weight), and P utilization efficiency of nonmycorrhizal tomato strains at low (0.008 mg P/liter soil solution) and high (0.031 mg P/ liter soil solution) P levels.

	MYCO. DAILY P UPTAKE (mg)[z]			MYCO. DAILY DRY WEIGHT (g)[w]			MYCO. PUE[y]	
STRAIN	high P(H)	low P(L)	L/H ratio	high P(H)	low P(L)	L/H ratio	low P	high P
7	5.91 bc[x]	5.56 abc	0.94 ab	3.62 ab	3.07 ab	0.85 b	553.8	615.3
8	4.06 d	3.34 d	0.82 ab	2.79 d	1.63 b	0.97 ab	481.1	415.3
43	5.76 bc	4.55 bcd	0.79 b	2.22 d	1.99 b	0.89 b	432.1	386.3
55	7.76 a	7.23 a	0.93 ab	2.96 bc	4.10 a	1.38 a	569.3	381.8
66	4.43 cd	3.72 cd	0.84 ab	2.21 d	1.82 b	0.83 b	491.7	499.5
159	6.52 ab	5.65 ab	0.87 ab	3.84 a	3.17 b	0.83 b	555.0	589.3
999	4.95 bcd	5.21 abc	1.05 a	2.38 cd	2.45 ab	1.03 ab	471.8	481.5
mean	5.61	2.63	0.89	2.67	2.61	0.97	507.7	481.3
CV	18.09	28.9	26.1	17.2	27.3	27.0		
r_s[v]	0.07	0.43	0.36	0.04	0.73	0.61	<u>0.75</u>	<u>0.89</u>

[x] Means followed by the same letter are not statistically different according to Fisher's 'protected' $LSD_{0.05}$.

[y] PUE = P utilization efficiency (mg dry weight produced per mg P uptake).

[z] Includes P accumulation in stems, leaves and fruit devided by days of growth.

[w] Includes dry weight accumulation in stems, leaves and fruit devided by days of growth.

[v] Spearman's rank correlation (Snedecor and Cochran, 1967) between mycorrhizal and nonmycorrhizal data. $P<0.05$ was underlined.

Lorenz and Tyler (1983) indicated that tissue P concentrations higher than 3.5 mg/g indicated sufficient soil P concentrations for tomato growth and tissue concentrations lower than 2.5 mg P /g were considered deficient. These guidelines suggested that the plants suffered only slight P deficiency.

Another complicating factor was the determination of the harvesting time. The strains in this experiment were harvested early, before the plants reached maximum production. Since strains had very different growth and fruiting habits (e.g. determinated and indeterminated types, cherry and noncherry type), comparable harvest periods between strains were very difficult to determine. In order to standardize the plant growth stage, dry weight and total P uptake data taken when the first flower opened and total plant growth at final harvest would be most accurate in assessing P tolerance.

CONCLUSIONS

Strains 43, 59 and 999 had the highest P uptake ratio (LP/HP P uptake) and were selected as low P tolerant strains in this field study. High total P uptake was the mechanism that mainly contributed to P efficiency with respect to dry weight accumulation in this study.

Mycorrhizal effects on P uptake ability depended on soil P level and the strains involved. Total P uptake of most strains was increased by mycorrhizal inoculation under both high P and low P conditions. The strains that responded the most to mycorrhizal inoculation tended to have low daily P uptake. However, some strains showed significantly decreased P uptake with mycorrhizae. Mycorrhizae may have competed with the plant for available P or carbohydrates.

In the present study, mycorrhizae affected the determination of low-P tolerant strains. Thus, the presence or absence of mycorrhizae should be noted when making recommendations on low P tolerant strains. However, mycorrhizal inoculation was an easy, low cost procedure to increase plant P uptake and the ability to grow under low P conditions. Therefore, the selection of low-P tolerant strains that also respond to mycorrhizal inoculation may be a good strategy to overcome the low productivity in low-P-available soils.

CHAPTER 4 COMPARISONS OF EXPERIMENTAL TECHNIQUES USED IN SCREENING FOR LOW PHOSPHORUS TOLERANT TOMATO STRAINS

INTRODUCTION

Field studies employing different levels of available P are difficult to establish, maintain, and reproduce. Barrow et al. (1977) found that available P changes over time, even in uncropped soil, making it difficult to produce equivalent P stress in repeated experiments. Developing screening methods in the greenhouse or lab that would correlate highly with field results would expedite the process of selecting low-P-tolerant tomato strains.

Several methods have been used to screen low-P-tolerant tomato strains. For example, tomato strains were screened in a sand-soil medium pot study in Chapter 2. Coltman et al. (1982) developed a sand-alumina medium for growth chamber evaluations of mechanisms involved in interspecific variation of P efficiency in tomato. Activated alumina was "loaded" into a media by exposure to different concentrations of KH_2PO_4 solutions in the greenhouse. Phosphorus concentrations in solutions expressed from sand-alumina mixtures were dependent upon the P concentrations used to absorb P onto the alumina. This system provided

stable and reproducible P concentrations, as well as simulated plant response to P in the soil.

Aseptic root culture also has been used to screen tomato germplasm for tolerance to P deficiency in the lab. Coltman (1987) germinated tomato strains in a sterile, liquid medium containing 2 levels of P (0.21 and 0.78 mg P per liter solution) and examined the growth of 1-cm-long root tips at these two levels. Phosphorus efficiencies of the different strains were determined by comparing relative root weight under P-deficient and P-sufficient conditions.

The question remains as to how well conclusions drawn from the above studies correlate with field results. In this chapter, results from the nonmycorrhizal treatment of the sand-soil study (Chapter 2), a sand-aluminum study (Coltman et al., 1982), and a root culture study (Coltman, 1987) are compared with results obtained in the nonmycorrhizal treatment of the field study of Chapter 3. The P uptake ratio (P uptake at low P/ P uptake at high P) (Table 4.3), dry weight ratio (dry weight at low P/ dry weight at high P) (Table 4.4), P utilization efficiency (Table 4.7), P uptake ability (Table 4.5), and dry weight accumulation ability (Table 4.6) under low P conditions were correlated amongst the four screening methods. The low-P tolerant strains were identified by relatively less growth

depression or decrease in P uptake under the P deficient condition. Therefore, the most meaningful comparisons to identify low-P tolerance are the ratios of P uptake and dry weight at low verses high P, and these parameters are emphasized in this chapter. The normal sample correlation (Snedecor and Cochran, 1967), were used to compare the methods.

Some adjustments to the data sets were made for calculating the correlations. For example, strain 214 has been found to lose its P uptake ability from solutions with pH higher than 6.0 (Coltman, personal communication). The sand-alumina system used for low-P-tolerance screening was strongly buffered at about pH 7. Therefore, the poor growth of strain 214 in sand-alumina should not be expected to occur in other screening media with lower pH. The inclusion of data on strain 214 thus might bias the correlation, and so data from this strain were omitted in the comparisons except in the comparison of P utilization efficiency. Plant P utilization efficiency did not affect by the plant P uptake. In order to focus on the low-P-tolerance performance in different soil systems, the tolerant and intolerant strains 7, 8, 43, 55, 159 and 999 from the field study were used in comparisons with the sand-soil pot study. These strains had similar P uptake at high P levels, but

dissimilar P uptake at low P levels in the field, and were used to identify low-P-tolerance mechanisms in Chapter 3.

The strains and methodological summary of the 4 studies are shown in Table 4.1 and 4.2. The data for comparison between various studies are shown in Appendix C to Appendix L.

COMPARISON OF FOUR EXPERIMENTAL METHODS

In comparing the four experimental methods, a number of significant correlations arose. In the sand-soil study, the P uptake ratio (low P/ high P) (r=-0.99), (Table 4.3), dry weight ratio (low P/high P), (r=-0.85) (Table 4.4) and P uptake (r=-0.88) (Table 4.5) were significantly negatively correlated to the same parameters in the field study at low P level. These two screening methods used same soil and similar soil P levels. Therefore, this two methods should have high correlation at screening results. However, the samples were taken during different growth stages at field and sand-soil pot study, which may have affected both the P uptake and dry weight ratios and caused the negative correlation between sand-soil and field study.

Fox et al. (1976) reported that the corn needed higher external P at early growth stage (0.2 mg P per liter) than the grain fill stage (0.06 mg P per liter) to reach optimal

Table 4.1. The tomato strains used in four low-P tolerant screening methods: field, sand-soil-pot, sand-alumina-pot and root liquid culture.

STRAIN	FIELD	SAND-SOIL POT	SAND-ALUMINUM POT	ROOT LIQUID CULTURE
2	*	*		*
7	*	*		
8	*	*		*
10	*	*		
11	*	*		*
12	*	*		*
13	*	*		
15	*	*		
16	*	*		
17	*	*		
20	*	*		
27	*	*		
35	*	*		*
37	*	*		*
43	*	*		*
55	*	*	*	
127	*	*	*	
134	*	*	*	
159	*	*	*	
212	*	*	*	
214	*	*	*	
479	*	*	*	
999	*	*		

Table 4.2. Differences in plant tissue, plant age, extractable P concentration in medium, growth medium and the place experiments were conducted for four low-P tolerant screening methods: field, sand-soil-pot, sand-alumina-pot and root liquid culture.

	METHODS			
CHARACTER	FIELD	SAND-SOIL POT	SAND-ALUMINUM POT	ROOT LIQUID CULTURE
TISSUE	SHOOT FRUIT	SHOOT	SHOOT	1-cm ROOT TIP
AGE(days)	80-95	24	19-24	19
P CONC. (mg P per liter soil solution)				
LP	0.008	0.01	0.31	0.21
HP	0.032	0.026	3.1	0.78
AVERAGE LEVEL OF LOW-P STRESS (1- low P/high P ratio)%				
DRY WEIGHT	5%	86%	about 50%	39%
P UPTAKE	19%	81%	about 50%	70%
MEDIUM	SOIL	SAND-SOIL	SAND-ALUMINA	NUTRIENT SOLUTION
CULTURE/ PLACE	- FIELD	POT/ GREENHOUSE	POT/ GROWTHCHAMBER	FLASK/ LABORATORY

Table 4.3. The correlation of P uptake ratio among four low-P tolerance screening methods: field, sand-soil-pot, sand-alumina-pot and root liquid culture.

P UPTAKE RATIO (P UPTAKE AT LOW P/ P UPTAKE AT HIGH P)

SCREENING METHOD	Correlation coefficient: SAND-SOIL r^z	Correlation coefficient: FIELD r^z
SAND-SOIL		<1>[q]
a) All strains in common (n=21)	-	-0.49
b) Selected strains (n=6)[x]	-	<u>-0.95</u>
SAND-ALUMINA[w]	<3>	<5>
a) Selected strains (n=6)[v]	0.56	0.05
ROOT CULTURE	<7>	<9>
a) All strains in common (n=7)[u]	-0.43	0.13

[z] Sample correlation coefficient (Snedecor and Cochran, 1967). P<0.05 in underlined.
[x] Strains differing in P efficiency in the field study: 7, 8, 43, 55, 159 and 999.
[w] Actual P uptake at low P is the correlated variable due to all of the strains having similar dry weight at the high P level.
[v] Strain 214 was omitted due to its anomolous behavior in sand-alumina.
[u] Strains differing in P efficiency in root culture: 2, 8, 11, 12, 35, 37 and 43.
[q] The index number for the actual data in Appendix table. <1> in Appendix C. <3> in Appendix D. <5> in Appendix E. <7> in Appendix F. <9> in Appendix G.

Table 4.4. The correlation of dry weight ratio among four low-P tolerance screening methods: field, sand-soil-pot, sand-alumina-pot and root liquid culture.

	DRY WEIGHT RATIO (DRY WEIGHT AT LOW P/ DRY WEIGHT AT HIGH P)	
	Correlation coefficient	
SCREENING METHOD	SAND-SOIL	FIELD
	r^z	r^z
SAND-SOIL	<2>[q]	
a) All strains in common (n=21)	-	-0.39
b) Selected strains (n=6)[x]	-	<u>-0.85</u>
SAND-ALUMINA[w]	<4>	<6>
b) Selected strains (n=6)[v]	0.34	-0.03
ROOT CULTURE	<8>	<10>
a) All strains in common (n=7)[u]	-0.53	0.46

[z] Sample correlation coefficient (Snedecor and Cochran, 1967). P<0.05 in underlined.
[x] Strains differing in P efficiency in the field study: 7, 8, 43, 55, 159 and 999.
[w] Actual dry weight at low P is the correlated variable due to all of the strains having similar dry weight at the high P level.
[u] Strains differing in P efficiency in root culture: 2, 8, 11, 12, 35, 37 and 43.
[q] The index number for the actual data in Appendix table. <2> in Appendix C. <4> in Appendix D. <6> in Appendix E. <8> in Appendix F. <10> in Appendix G.

Table 4.5. The correlation of P uptake among four low-P tolerance screening methods: field, sand-soil-pot, sand-alumina-pot and root liquid culture.

	P UPTAKE			
	Correlation coefficient			
SCREENING METHOD	SAND-SOIL		FIELD	
		r^z		r^z
SAND-SOIL			<11>[w]	
a) All strains in common (n=21)		-		-0.21
b) Selected strains (n=6)[x]		-		<u>-0.99</u>
SAND-ALUMINA	<14>		<17>	
a) Selected strains (n=6)[v]		0.63		<u>-0.82</u>
ROOT CULTURE	<20>		<23>	
a) All strains in common (n=7)[u]		-0.29		-0.60

[z] Sample correlation coefficient (Snedecor and Cochran, 1967). P<0.05 in underlined.
[x] Strains differing in P efficiency in the field study: 7, 8, 43, 55, 159 and 999.
[u] Strains differing in P efficiency in root culture: 2, 8, 11, 12, 35, 37 and 43.
[v] Strain 214 was omitted due to its anomolous behavior in sand- alumina.
[w] The index number for the actual data in Appendix table. <11> in Appendix H. <14> in Appendix I. <17> in Appendix J. <20> in Appendix K. <23> in Appendix L.

growth. In the sand-soil pot study, the P uptake of 24 day old plant at 0.027 mg P/liter soil solution (high P level) was highly correlated with P uptake of about 80 day old plant at 0.01 mg P/ liter soil solution P (low P level) ($r=0.88$, $P<0.01$), (Appendix M). Dry weights had similarly highly correlated ($r=0.97$, $P<0.01$), (Appendix N). A possible explanation for this correlation is that 24 days old plant at high P level (0.027 mg P/liter soil solution P) in the sand-soil study may have suffered similar P deficiency as the 80 day old plants grown at the low P level (0.008 mg P/liter soil solution) in the field. As mentioned in chapter 2, all the strains at the high P level (0.027 mg P/liter soil solution) had low tissue P concentrations. Thus, plants grown at the high P level in sand-soil pot study probably grew under moderate P stress.

At the low P level (0.01 mg P/ liter soil solution), all the strains had very low tissue P concentrations, and grew very slowly in the sand-soil study. The low P level of 0.01 mg P/liter soil solution may have been so low that almost no differences between strains were observed in this pot study. However, the low-P tolerant strains may have grown better and take up more P than the intolerant strains at the higher but still deficient "high P" level of 0.027 mg P/liter. The low-P tolerant strains, therefore, had the

lower low P/ "high P" dry weight ratios and P uptake ratios than the intolerant strains and this may have caused a significant negative correlation between the soil-sand and the field study.

Because the sand-soil study may have lacked a P level which produced optimal plant growth, low-P tolerance cannot be evaluated by the dry weight and P uptake ratio in this study. Therefore, comparison of dry weight and P uptake ratio between sand-soil pot study and the field study are meaningless. However, the dry weight and P uptake of the sand-soil study at the "high P" level correlated highly with the field study at the low P level. Sand-soil studies may yield accurate low-P tolerant screening results in the appropriate soil P level.

The dry weights of the soil-sand study also were negatively correlated with the low P level in the root culture ($r=-0.77$) (Table 4.6). The reasons for this relation are unclear. However, the low correlations of dry weight and P uptake ratios between the root culture and field studies suggest that the root culture technique may not be a very good method to evaluate P tolerant strains.

The comparison between sand-alumina and field studies also demonstrated a significant negative correlation in dry weight ($r=-0.87$, $P<0.01$) (Table 4.6) and in P uptake ($r=$

Table 4.6. The correlation of dry weight among four low-P tolerance screening methods: field, sand-soil-pot, sand-alumina-pot and root liquid culture.

	DRY WEIGHT	
	Correlation coefficient	
SCREENING METHOD	SAND-SOIL	FIELD
	r^z	r^z
SAND-SOIL		<13>[W]
A) ALL strains in common (n=21)	-	-0.21
b) Selected strains (n=6)[x]	-	-0.52
SAND-ALUMINA[W]	<16>	<19>
b) Selected strains (n=6)[v]	0.42	<u>-0.87</u>
ROOT CULTURE	<22>	<25>
a) All strains in common (n=7)[u]	<u>-0.77</u>	-0.56

[z] Sample correlation coefficient (Snedecor and Cochran, 1967). P<0.05 in underlined.
[x] Strains differing in P efficiency in the field study: 7, 8, 43, 55, 159 and 999.
[v] Strain 214 was omitted due to its anomolous behavior in sand-alumina.
[u] Strains differing in P efficiency in root culture: 2, 8, 11, 12, 35, 37 and 43.
[W] The index number for the actual data in Appendix table. <13> in Appendix H. <16> in Appendix I. <19> in Appendix J. <22> in Appendix K. <25> in Appendix L.

-0.82, P<0.05) (Table 4.5). Except the strain 127 had relative low dry weight and P uptake, all the other strains had very similar dry weight and P uptake at low P level in the sand-alumina study. However, strain 127 had best growth among all strains in field study, when the other strains had similar growth with each other. The differently relative performance of strain 127 at field and sand-alumina study created the high negative correlation of low P dry weight and P uptake between this two study. Therefore, this correlation does not suggest a useful relationship for comparing the field and sand-soil study.

The low correlations of dry weight and P uptake ratios between the sand-alumina and field studies suggest that the sand-alumina method may not be a very good method to evaluate P tolerant strains. However, P utilization efficiency in the sand-alumina study correlated highly with that in the field study (P< 0.08) (Table 4.7). This suggests that the sand-alumina study may be useful in screening for high P utilization efficiency strains.

In general, tomato strains responded quite differently to low phosphorus conditions from one study to another. Most of the comparisons showed low correlations amongst the methods (Table 4.3 to 4.7). Possible explanations for the low correlation between the experiments include differences

Table 4.7. The correlation of P utilization efficiency of four low P tolerance screening methods: field, sand-soil-pot, sand-alumina-pot and root liquid culture.

	P UTILIZATION EFFICIENCY	
	Correlation coefficient	
SCREENING METHOD	SAND-SOIL	FIELD
	r^z	r^z
SAND-SOIL		<27>[w]
a) All strains in common (n=21)	-	0.41
b) Selected strains (n=6)[x]	-	0.52
SAND-ALUMINA	<15>	<18>
a) Selected strains (n=7)	-0.02	0.68*
ROOT CULTURE	<21>	<24>
a) All strains in common (n=7)[u]	-0.50	-0.51

[z] Sample correlation coefficient (Snedecor and Cochran, 1967). P<0.05 in underlined.
[x] Strains differing in P efficiency in the field study: 7, 8, 43, 55, 159 and 999.
[u] Strains differing in P efficiency in root culture: 2, 8, 11, 12, 35, 37 and 43.
* P<0.08.
[w] The index number for the actual data in Appendix table. <12> in Appendix H. <15> in Appendix I. <18> in Appendix J. <21> in Appendix K. <24> in Appendix H.

in plant materials and growing conditions. The sand-soil and sand-aluminum pot studies examined young shoots and roots, but mature stems and fruits was used in field study, and 1 cm-long root tips were used in the root culture study. This difference in tissues and plant age may contributed to the poor correlation among the experiments. However, even if the same tissues were sampled at the same time in greenhouse and field studies, no correlation may be found. Caradus et al. (1986) examined clover leaves at the same age in the greenhouse and in the field, and found very low correlations between dry weights and dry weight ratios.

Differences in growing conditions can have marked effects on the plant's response to P. Finne and Mack (1964) found that the ranking of four cultivars of Dactylis glomerata for P uptake from soil depended on soil water content and temperature. In a field planting, Jessop (1974) evaluated 17 wheat strains for low-P tolerance over two consecutive years. He found that tolerant strains identified in the first year were different from strains identified in the second. He suggested climatic differences caused this poor relationship. Caradus and Snaydon (1986) further concluded that environment had an overriding influence on determining low-P tolerant strains. Therefore,

conclusions from screening experiments appear to be restricted to the environments in which they were conducted.

Appendix A.
The U.S. Plant Introduction number, place of origin and other identification of Lycopersicon esculentum strains that were evaluated for low-P tolerance in sand-soil pot and field study.

ACC	PLANT INTRO	SOURCE	OTHER IDENTIFICATION
2		AVRDC	
7		AVRDC	
8		AVRDC	
10	091909	Bulgaria	UW#7/O'sull#109
11	092859	China	UW#23/O'sull#114
12	092863	Manchruia	UW#27/O'sull#115
13	106997	Brit.Guiana	UW#61/O'sull#132
15	114966	Egypt	UW#96/O'sull#139
16	117897	Brazil	UW#115/O'sull#145
17	117900	Brazil	UW#118/O'sull#146
20	367939	Brazil	UW#460/O'sull#79/BGH 160
27	326173	South Africa	UW#563/O'sull#14
35	304228	USA-NY	Thick Sepal
37	309666	USA-IN	Epoch
43	338492	Bulgaria	Bali??n
48	345561	USSR	Push Kinsky 1853
49	79532	Peru	Pan America
50	109315	Turkey	
51	126408	Panama	
52	127805	Peru	
54	203229	Australia	Manzaua
55	203230	Australia	Rey de los tempranos
56	262930	USSR	Gruntay staospely 1165
57	262930	USSR	Maliuta 101
58	265956	USA-HI	Kdes C
59	265957	USA-HI	
60	270213	USA-MI	Victor
61	271381	India	Paipur
62	280595	USSR	Delikates
64	283916	Czechoslovakia	Jubileum
65	283922	Czechoslovakia	Kecshemeti torpe
66	285068	Dhilippines	Nagcarlau
67	285132	USA-OK	Bearwell
68	288069	Great Britaiw	Open Air
69	289204	Hungary	Canadienne Menael
70	289252	Hungary	Cromco
71	294439	Israel	
127	367941	Brazil	BGH 70 / UW#462/O'sull#51
134	367958	Brazil	BGH 218 / UW#472/O'sull#60/64
159	273029	Guatemala	UW#504/O'sull#22
212	126407	Panama	
214	126409	Peru	
479	367966	Brazil	
999		USA, Hawaii	Oahu

Appendix B-1.

The nonmycorrhizal inoculated treatments of 31 tomato strains of whole plant, stem and fruit dry weight and fruit/shoot dry weight ratio at high (0.031 mg P/liter soil solution) and low (0.008 mg P/ liter soil solution) P levels in field study.

	NONMYCO. HIGH P DRY WEIGHT				NONMYCO. LOW P DRY WEIGHT			
STRAIN	whole[x]	stem(S)	fruit(F)	F/S	whole	stem(S)	fruit(F)	F/S
2	4.14	2.31	1.84	0.85	4.40	2.65	1.75	0.65
7	3.69	2.75	0.94	0.36	2.80	1.90	0.90	0.49
8	2.49	1.58	0.91	0.61	1.30	0.79	0.52	0.70
10	4.34	2.76	1.31	0.44	2.93	1.76	1.17	0.69
11	3.62	2.40	1.22	0.51	3.27	2.51	0.76	0.33
12	3.98	3.47	0.50	0.14	3.90	2.96	0.94	0.38
13	5.92	4.41	1.50	0.35	7.34	5.75	1.59	0.29
15	2.42	1.14	1.28	1.27	2.82	1.85	0.98	0.53
16	2.43	1.57	0.86	0.59	2.91	1.75	1.16	0.72
17	4.83	3.47	1.36	0.40	4.01	2.59	1.20	0.43
20	3.55	2.42	1.12	0.53	3.07	2.15	0.92	0.43
27	1.84	1.20	0.65	0.57	2.11	1.36	0.76	0.58
35	1.73	0.79	0.94	1.13	1.30	0.70	0.61	0.92
37	0.77	0.64	0.14	0.23	0.91	0.78	0.13	0.19
43	2.52	1.22	1.30	1.10	2.80	1.39	1.41	1.08
48	2.68	1.16	1.52	1.35	3.21	1.50	1.70	1.15
55	2.77	1.41	1.36	1.00	3.32	1.77	1.55	1.14
58	3.83	1.92	1.91	1.06	3.09	1.45	1.65	1.13
59	2.08	1.29	0.79	0.68	2.80	1.57	1.24	0.84
60	1.64	0.61	1.02	2.05	1.52	0.50	1.03	2.07
61	2.04	1.16	0.89	0.84	2.59	1.43	1.15	0.82
66	3.75	1.65	2.10	1.27	2.09	0.79	1.31	1.72
68	2.64	1.37	1.27	0.92	2.23	1.02	1.21	1.26
70	2.04	0.97	1.07	1.15	1.88	0.68	1.20	1.81
127	6.20	2.62	3.58	1.40	5.08	2.19	2.89	1.34
134	3.99	2.60	1.39	0.53	3.02	1.52	1.50	1.19
159	3.55	2.66	0.90	0.34	2.92	2.04	0.88	0.47
212	6.36	4.74	1.62	0.40	3.50	2.35	1.15	0.55
214	3.10	2.51	0.59	0.27	2.57	1.94	0.63	0.30
479	2.41	1.30	1.11	0.95	2.16	1.30	0.87	0.70
999	3.17	1.41	1.76	1.40	3.73	1.70	2.03	1.22
MEAN	3.24	1.95	1.25	0.80	2.95	1.73	1.19	0.84

[x] whole= stems plus fruits.

Appendix B-2.

The mycorrhizal inoculated treatments of 31 tomato strains of whole plant, stem and fruit dry weight and fruit/shoot dry weight ratio at high (0.031 mg P/liter soil solution) and low (0.008 mg P/liter soil solution) P levels in field study.

	MYCO. HIGH P DRY WEIGHT				MYCO. LOW P DRY WEIGHT			
STRAIN	wholex	stem(S)	fruit(F)	F/S	whole	stem(S)	fruit(F)	F/S
2	4.81	2.69	2.12	0.82	3.28	1.72	1.56	0.90
7	3.62	2.41	1.21	0.50	3.07	1.93	1.14	0.59
8	1.69	0.95	0.75	0.84	1.63	1.03	0.60	0.64
10	2.86	1.68	1.18	0.73	2.88	1.74	1.14	0.64
11	3.56	2.62	0.94	0.38	3.15	2.15	0.99	0.46
12	3.80	3.06	0.71	0.23	4.39	3.82	0.57	0.15
13	8.76	7.45	1.30	0.20	7.68	6.18	1.50	0.25
15	3.05	2.00	1.06	0.55	2.29	1.36	0.93	0.78
16	4.33	2.38	1.95	0.82	3.00	1.85	1.15	0.61
17	3.64	2.61	1.03	0.42	3.07	1.88	1.19	0.63
20	3.07	2.33	0.74	0.32	3.58	2.09	1.22	0.52
27	2.23	1.37	0.86	0.64	1.73	1.11	0.62	0.57
35	1.75	0.78	0.97	1.28	1.50	0.76	0.74	1.00
37	0.90	0.78	0.13	0.18	0.69	0.54	0.14	0.24
43	2.22	1.19	1.03	0.88	1.98	0.96	1.02	1.10
48	3.17	1.45	1.72	1.22	3.12	1.27	1.85	1.46
55	2.96	1.78	1.19	0.68	4.10	2.44	1.66	0.67
58	3.13	1.57	1.56	1.00	2.39	1.22	1.17	0.97
59	3.14	1.67	1.47	0.95	3.32	2.06	1.25	0.68
60	1.91	0.66	1.25	1.99	1.36	0.39	0.98	2.80
61	1.89	1.30	0.59	0.47	2.64	1.47	1.17	0.83
66	2.21	0.84	1.37	1.62	1.82	0.76	1.06	1.40
68	4.76	2.38	2.37	1.01	2.96	1.50	1.46	0.95
70	2.14	1.13	0.96	0.95	2.66	1.28	1.39	1.11
127	6.93	3.02	3.91	1.32	4.85	1.74	3.10	1.84
134	2.57	1.40	1.17	1.16	2.25	1.39	0.86	0.71
159	3.84	2.84	1.00	0.36	3.17	2.34	0.83	0.43
212	4.76	3.18	1.58	0.68	3.40	2.57	0.83	0.35
214	2.83	2.20	0.63	0.31	3.35	2.71	0.64	0.24
479	3.72	2.02	1.71	0.84	3.18	1.71	1.46	0.85
999	2.38	1.07	1.31	1.35	2.45	1.10	1.36	1.25
MEAN	3.31	1.98	1.28	0.80	2.93	1.74	1.15	0.81

x whole= stems plus fruits.

Appendix C.
<1>, <2> The comparison of P uptake ratio and dry weight ratio between the sand-soil-pot study and the field study at low P.

STRAIN	<1> P UPTAKE RATIO[z] Sand-Soil	Field	<2> DRY WEIGHT RATIO[y] Sand-Soil	Field
2	0.15	0.93	0.17	1.06
7 * [u]	0.21	0.67	0.22	0.76
8 *	0.23	0.46	0.30	0.52
10	0.12	0.81	0.16	0.72
11	0.10	0.77	0.14	0.90
12	0.17	0.89	0.20	0.98
13	0.10	0.78	0.15	1.24
15	0.20	0.73	0.24	1.17
16	0.15	0.94	0.20	1.19
17	0.14	0.74	0.19	0.78
20	0.18	0.58	0.28	0.87
27	0.12	0.95	0.18	1.15
35	0.12	0.62	0.17	0.76
37	0.08	0.76	0.14	1.18
43 *	0.09	1.03	0.15	1.11
55 *	0.11	0.86	0.20	1.20
127	0.09	0.81	0.14	0.82
134	0.17	0.72	0.21	0.76
159 *	0.15	0.69	0.28	0.82
212	0.13	0.50	0.19	0.55
214	0.15	0.91	0.22	0.83
479	0.14	0.84	0.19	0.90
999 *	0.08	1.08	0.14	1.18
mean	0.14	0.81	0.19	0.95
	r = -0.49		r= -0.39	
	r(x)[v]= -0.95		r(x)= -0.85	

[z] P uptake ratio = P uptake at low P vers. high P.
[y] Dry weight ratio = dry weight at low P vers high P;
[u] Selected strains. These strains had similar P uptake at high P and dissimilar P uptake at low P and represent the tolerant and intolerant strains in field study.
[w] Sample correlation coefficient (Snedecor and Cochran, 1967) of all strains between the sand-soil and the field.
[v] Sample correlation coefficient (Snedecor and Cochran, 1967) of selected strains between the sand-soil and the field.

Appendix D.

<3>, <4> Comparison of P uptake ratio and dry weight ratio between the sand-alumina-pot and sand-soil-pot studies.

	<3>		<4>	
Strain	P UPTAKE Sand-Al	P UPTAKE RATIO Sand-Soil	DRY WEIGHT Sand-Al	DRY WEIGHT RATIO Sand-Soil
55	17.1 ab[y]	0.11 a	6.89 bc	0.20 a
134	15.7 bc	0.17 a	6.83 bc	0.21 a
159	14.5 c	0.15 a	6.44 c	0.28 a
212	16.1 bc	0.13 a	7.40 ab	0.19 a
479	18.4 a	0.14 a	7.98 a	0.19 a
127	11.0 d	0.09 a	4.91 d	0.14 a
214	9.8 d	0.15 a	4.59 d	0.22 a
mean	14.7	0.13	6.38	0.38
	r(x)[v]= 0.55		r(x)= 0.34	

[y] Mean separation at each P level by LSD, P=5%.
[v] Sample correlation coefficient (Snedecor and Cochran, 1967) of selected strains between the sand-alumina and the sand-soil.

Appendix E.

<5>, <6> Comparison of P uptake ratio and dry weight ratio between the sand-alumia-pot study and the field study.

	<5>		<6>	
STRAIN	P UPTAKE Sand-Al	P UPTAKE RATIO Field	DRY WT. Sand-Al	DRY WT. RATIO Field
55	17.1 ab[u]	0.86 a	6.89 bc	1.20 a
134	15.7 bc	0.72 ab	6.83 bc	0.76 b
159	14.5 c	0.69 ab	6.44 c	0.82 b
212	16.1 bc	0.50 b	7.40 ab	0.55 c
479	18.4 a	0.84 a	7.98 a	0.90 ab
127	11.0 d	0.81 a	4.91 d	0.82 b
214	9.8 d	0.91 a	4.59 d	0.83 b
mean	14.7	0.72	6.38	0.84
	$r(x)^{v}$= 0.05		r(x)= -0.03	

[u] Mean separation at each P level by LSD, P=5%.
[v] Sample correlation coefficient (Snedecor and Cochran, 1967) of selected strains between the sand-alumina and the sand-soil.

Appendix F.

<7>, <8> Comparison of P uptake ratio and weight ratio between the root culture and the sand-soil pot studies at low P.

	<7> P UPTAKE RATIO[x]		<8> WEIGHT RATIO	
STRAIN	Root-Culture	Sand-Soil	Root[y]-Culture	Sand-Soil[w]
8	0.31	0.23 a[z]	0.47 b	0.30 a
2	0.29	0.15 bc	0.52 b	0.17 b
12	0.30	0.17 ab	0.45 b	0.20 b
11	0.30	0.10 cd	0.51 b	0.14 b
43	0.34	0.09 cd	0.71 a	0.15 b
35	0.32	0.12 c	0.68 a	0.17 b
37	0.32	0.08 d	0.80 a	0.14 b
mean	0.59	0.14	0.59	0.18
	r^{v}= -0.43		r= -0.53	

[x] P UPTAKE RATIO= P uptake at low P/ P uptake at high P.
[y] Fresh root weight at low P/ fresh root weight at high P.
[w] Shoot dry weight at low P/ shoot dry weight at high P.
[z] Mean separation at each P level by LSD, P=5%.
[v] Sample correlation coefficient (Snedecor and Cochran, 1967) of all strains between the root culture and the sand-soil.

Appendix G.

<9>, <10> Comparison of P uptake ratio and weight ratio between the root culture and the field studies at low P.

	<9> P UPTAKE RATIO[x]		<10> WEIGHT RATIO	
STRAIN	Root-Culture	Field	Root-Culture[y]	Field[w]
8	0.31	0.46 c[z]	0.47 b	0.53 b
2	0.29	0.93 a	0.52 b	1.13 a
12	0.30	0.89 ab	0.45 b	0.94 ab
11	0.30	0.77 ab	0.51 b	0.90 ab
43	0.34	1.02 a	0.71 a	1.12 a
35	0.32	0.62 bc	0.68 a	0.92 ab
37	0.32	0.76 ab	0.80 a	1.16 a
mean	0.59	0.78	0.59	0.94
	r^{v}= 0.13		r= 0.46	

[x] P UPTAKE RATIO= P uptake at low P/ P uptake at high P.
[y] Fresh root weight at low P/ fresh root weight at high P.
[w] Shoot dry weight at low P/ shoot dry weight at high P.
[z] Mean separation at each P level by LSD, P=5%.
[v] Sample correlation coefficient (Snedecor and Cochran, 1967) of all strains between the root culture and the field.

Appendix H.
<11>, <12>, <13> Comparison of P uptake, P utilization efficiency and dry weight between the sand-soil-pot study and the field study at low P.

		<11> P UPTAKE (mg)		<12> PUE[y]		<13> DRY WEIGHT (g)	
STRAIN		Sand-soil	Field	Sand-soil	Field	Sand-soil	Field
2		5.87	11.31	658	389	3.87	4.40
7	* [u]	6.82	4.07	688	687	4.70	2.80
8	*	7.74	2.68	531	485	4.11	1.30
10		5.00	4.90	756	596	3.78	2.92
11		4.45	4.72	838	691	3.73	3.26
12		5.49	7.95	764	490	4.20	3.90
13		3.56	12.85	796	571	2.83	7.33
15		7.02	4.17	796	675	5.60	2.82
16		4.09	4.18	893	694	3.65	2.90
17		5.31	8.86	790	427	4.20	3.78
20		9.69	5.98	736	513	7.13	3.07
27		6.73	4.63	718	456	4.83	2.11
35		3.93	2.98	854	436	3.36	1.30
37		3.72	1.71	759	529	2.82	0.90
43	*	5.16	6.21	660	450	3.41	2.79
55	*	5.79	5.53	847	600	4.91	3.31
127		3.72	9.15	779	554	2.90	5.07
134		9.22	6.72	562	449	5.18	3.02
159	*	6.07	4.50	1025	648	6.22	2.91
212		6.00	4.64	726	752	4.36	3.49
214		7.02	4.06	778	632	5.46	2.57
479		7.28	3.92	614	551	4.47	2.16
999	*	4.25	7.37	811	506	3.45	3.73
mean		5.82	5.51	756	548	4.32	2.95
		r^{w}= -0.21		r= 0.41		r= -0.21	
		$r(x)^{v}$= -0.99		r(x)= 0.52		r(x)= 0.52	

[y] PUE = P utilization efficiency.
[u] Strains selected for small data set analysis. These strains had similar P uptake at high P and dissimilar P uptake at low P and represent the tolerant and intolerant strains in field study.
[w] Sample correlation coefficient (Snedecor and Cochran, 1967) of all strains between the sand-soil and field.
[v] Sample correlation coefficient (Snedecor and Cochran, 1967) of selected strains between the sand-soil and the field.

Appendix I.

<14>, <15>, <16> Comparison of P uptake, P utilization efficiency and dry weight between the sand-alumina-pot and the sand-soil-pot studies at low P.

	<14> P UPTAKE (mg)		<15> PUE[u]		<16> DRY WEIGHT (g)	
STRAIN	Sand-Al	Sand-Soil	Sand-Al	Sand-Soil	Sand-Al	Sand-Soil
55	17.1 ab[y]	5.79 ab	438 a	806 b	6.89 bc	4.9 ab
134	15.7 bc	9.22 a	429 cd	571 c	6.83 bc	5.2 ab
159	14.5 c	6.07 ab	446 bc	990 a	6.44 c	6.2 a
212	16.1 bc	6.00 ab	465 ab	725 b	7.40 ab	4.4 ab
479	18.4 a	7.29 ab	438 bc	599 c	7.98 a	4.5 ab
127	11.0 d	3.72 b	465 ab	781 b	4.91 d	2.9 b
214	9.8 d	7.02 ab	478 a	781 b	4.59 d	5.5 ab
mean	14.7	5.5	446	650	6.38	4.8
	r(x)[v]= 0.63		r[z]= -0.06		r(x)= 0.42	

[u] PUE = P utilization efficiency, milligrams of dry weight per mg of P.
[y] Mean separation at each P level by LSD, P=5%.
[v] Sample correlation coefficient (Snedecor and Cochran, 1967) of selected strains between the sand-alumina and the sand-soil.
[z] Sample correlation coefficient (Snedecor and Cochran, 1967) of all strains between the sand-alumina and the sand-soil.

Appendix J.

<17>, <18>, <19> Comparison of P uptake, P utilization efficiency and dry weight between the sand-alumina-pot study and the field study at low P.

	<17> P UPTAKE (mg)		<18> PUE[y]		<19> DRY WEIGHT (g)	
STRAIN	Sand-Al	Field	Sand-Al	Field	Sand-Al	Field
55	17.1 ab[u]	5.5 b	438 a	597 bc	6.89 bc	3.32 b
134	15.7 bc	6.7 ab	429 cd	453 d	6.83 bc	3.02 b
159	14.5 c	4.5 b	467 bc	668 ab	6.44 c	3.18 b
212	16.1 bc	4.6 b	465 ab	744 a	7.40 ab	3.22 b
479	18.4 a	3.9 b	438 bc	551 c	7.98 a	2.16 b
127	11.0 d	9.2 a	465 ab	555 c	4.91 d	5.08 a
214	9.8 d	4.1 b	478 a	642 b	4.59 d	2.57 b
mean	14.7	5.5	446	604	6.38	3.22
	r(x)[v]= -0.82		r(x)= 0.71		r(x)= -0.87	

[y] PUE = P utilization efficiency, milligrams of dry weight per mg of P.
[u] Mean separation at each P level by LSD, P=5%.
[v] Sample correlation coefficient (Snedecor and Cochran, 1967) of selected strains between the sand-alumina and the field

Appendix K.

<20>, <21>, <22> Comparison of P uptake, P utilization efficiency and dry weight between the root liquid culture and the sand-soild studies at low P.

	<20> P UPTAKE (mg)		<21> PUE[x]		<22> WEIGHT (g)	
STRAIN	Root-Culture	Sand-Soil	Root-Culture	Sand-Soil	Root-Culture FW[y]	Sand-Soil DW[z]
8	9.0 bc	7.74 a	1129 ab	542 c	86 bc	0.41 ab
2	8.1 e	5.87 ab	1196 a	704 abc	83 c	0.39 ab
12	8.5 de	5.49 b	975 c	766 ab	69 d	0.42 a
11	8.7 cd	4.46 b	1012 bc	869 a	78 cd	0.37 ab
43	9.9 a	5.16 b	1206 a	695 bc	104 a	0.34 ab
35	9.2 b	3.93 b	1084 abc	808 a	91 bc	0.34 ab
37	9.4 b	3.72 b	1199 a	778 ab	98 ab	0.28 b
mean	9.0	5.19	1114	726	87	0.37
	r[v]= -0.29		r= -0.50		r= -0.77	

[x] PUE = P utilization efficiency, milligrams of dry weight per mg of P.
[y] FW = fresh weight.
[z] DW = dry weight.
[w] Mean separation at each P level by LSD, P=5%.
[v] Sample correlation coefficient (Snedecor and Cochran, 1967) of all strains between the root culture and the sand-soil.

Appendix L.

<23>, <24>, <25> Comparison of P uptake, P utilization efficiency and dry weight between the root liquid culture and the field studies at low P.

	<23> P UPTAKE (mg)		<24> PUE[x]		<25> WEIGHT (g)	
STRAIN	Root-Culture	Field	Root-Culture	Field	Root-Culture FW[y]	Field DW[z]
8	9.0 bc[w]	2.68 e	1129 ab	480 bc	86 bc	0.91 d
2	8.1 e	11.30 a	1196 a	392 d	83 c	4.42 a
12	8.5 de	8.00 b	975 c	485 bc	69 d	3.93 ab
11	8.7 cd	4.72 cd	1012 bc	687 a	78 cd	3.27 bc
43	9.9 a	6.2 bc	1206 a	449 c	104 a	2.80 c
35	9.2 b	2.99 de	1084 abc	434 cd	91 bc	1.31 d
37	9.4 b	1.72 e	1199 a	526 b	98 ab	0.91 d
mean	9.0	5.37	1114	497	87	2.56
	r^{v}= -0.60		r= -0.51		r= -0.56	

[x] PUE = P utilization efficiency, milligrams of dry weight per mg of P.
[y] FW = fresh weight.
[z] DW = dry weight.
[w] Mean separation at each P level by LSD, P=5%.
[v] Sample correlation coefficient (Snedecor and Cochran, 1967) of all strains between the root culture and the field.

Appendix M.

Comparison of P uptake at high P and low P, and P uptake ratio between the sand-soil pot study and the field study.

	Sand-Soil			Field		
	P UPTAKE		L/H RATIO	P UPTAKE		L/H RATIO
STRAIN	HIGH P(H)	LOW P(L)		HIGH P(H)	LOW P(L)	
7	32.5 c[x]	6.8 a	0.21 a	6.06 a	4.07 ab	0.67 bc
8	34.1 c	7.7 a	0.23 a	5.80 a	2.69 c	0.46 c
43	57.9 a	5.2 b	0.09 a	6.04 a	6.21 ab	1.03 a
55	51.0 ab	5.8 ab	0.11 a	6.41 a	5.53 a	0.86 ab
159	41.7 bc	6.1 ab	0.15 a	6.48 a	4.50 ab	0.69 bc
999	53.6 ab	4.9 b	0.08 a	6.84 a	7.37 a	1.08 a
mean	43.2	5.8	0.14	6.36	4.94	0.88

[x] Mean separation at each P level by LSD, P=5%.

Appendix N.

Comparison of dry weight at high P and low P, and P uptake ratio between the sand-soil-pot study and the field study.

	Sand-Soil			Field		
	DRY WEIGHT		L/H RATIO	DRY WEIGHT		L/H RATIO
STRAIN	HIGH P(H)	LOW P(L)		HIGH P(H)	LOW P(L)	
7	2.16 a[x]	0.47 b	0.22 b	3.69 ab	2.80 cd	0.76 c
8	1.39 b	0.41 bc	0.30 a	2.49 c	1.30 d	0.52 c
43	2.23 a	0.34 c	0.15 b	2.52 c	2.80 ab	1.11 ab
55	2.42 a	0.49 b	0.20 b	2.77 bc	3.32 abc	1.20 a
159	2.24 a	0.62 a	0.28 b	3.55 ab	2.92 bcd	0.82 bc
999	2.39 a	0.35 c	0.14 b	3.17 ab	3.73 a	1.18 a
mean	2.32	0.43	0.21	3.14	2.71	0.93

[x] Mean separation at each P level by LSD, P=5%.

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